THE STRUCTURAL DYNAMICS OF A TIDAL FLAT MOLLUSC COMMUNITY

by

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D. Woodward

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SUMMARY

1. A transect survey of the tidal flat mollusc community in the coastal Pipe Clay Lagoon, south-eastern Tasmania, was conducted over four seasons. The survey was conducted along a 700 m transect running down the tidal gradient from EHWS to MLW. In each season a 'distribution' transect was conducted with single quadrat (0.25 m x 0.25 m) samples being taken down to the anoxic layer every 20 m. At the same time a 'dispersion' transect was taken; every 100 m a grid (0.5 m x 0.5 m) consisting 8 x 8 cells was sampled down to the anoxic layer. A number of physical variables were also measured.

2. All molluscs and anemones that were retained by 0.5 mm mesh were defined to make up the community. The community comprised:

i. three suspension feeding bivalves - *Anapella cycladea*, *Katelysia scalarina* and *Wallucina assimilis*,

ii. one deposit feeding bivalve - *Soletellina biradiata*,

iii. two deposit feeding gastropods - *Hydrococcus brazieri* and *Salinator fragilis*,

iv. six algivorous gastropods - *Zeacumantus diemenensis*, *Rissopsis consobrina*, *Microdiscula charopa*, *Bembicium auratum*, *Austrocochlea constricta* and *Notoacmea alta*,

v. two carnivorous gastropods - *Cylichnina pygmaea* and *Nassarius pauperatus*,

vi. one parasitic gastropod - *Agatha metcalfei*

and vii. one carnivorous anemone - *Anthopleura aureoradiata*.

3. Statistical analysis of the survey data, followed by caging manipulation experiments, was used in an attempt to identify the principal factors responsible for controlling the structure of the community.

4. The survey provided information on the habitat and on the spatial and demographic patterns of the species. The habitat proved to be very stable. The beach profile showed little change throughout the sampling period and there were no obvious sediment sorting gradients over the transects.

5. The habitat stability was reflected in the relative stability of the populations making up the community. Species did not exhibit marked changes in either distribution or abundance from season to season, apart from those associated with recruitment.

6. The tidal gradient was the overriding environmental parameter and it appeared to exert its strongest influence on the species during their recruitment. Reproductive

patterns varied both between and within species according to the position on the beach. In most species, recruitment appeared to be virtually continuous although considerable temporal variations occurred. Generally, bivalve recruitment was greatest over the cooler months of the year and reproductive success, as measured by settled juveniles, tended to increase in high beach areas during the cooler months. The gastropods appeared to be less sensitive to desiccatory stress and their principal period of recruitment was over spring and summer.

7. The spatial and temporal variations in the structure of the community allowed a working hypothesis to be proposed. The structure of the community could be explained by a linking of the trophic group amensalism hypothesis of Rhoads and Young (1970) and Huston's (1979) dynamic equilibrium hypothesis for the maintainance of species diversity. It appeared that trophic group amensalism, acting on juvenile animals, was the major factor controlling the observed changes in community structure along the transects. Apart from *Anthopleura*, predators did not play a major role in determining the community structure.

8. A systematic analysis of the survey data, using serial and planar correlation analysis, followed by caging manipulation experiments, was used in an attempt to test the working hypothesis in three stages, each stage having successively greater fidelity.

9. The factors that appear to be responsible for the maintenance of the community structure can be outlined as follows:

i. The deposit feeding gastropods, *Hydrococcus* and *Salinator*, can tolerate a wide range of conditions, are distributed over most of the beach and compete for trophic resources. The two species show competitive exclusion in areas of high densities. Their feeding activities rework the substrate, making the sediment-water interface unstable.

ii. Larvae of the suspension feeding bivalves, *Anapella* and *Katelysia*, settle indiscriminantly on the substrate but are unable to survive in areas of highly reworked sediment. In areas where there are relatively low densities of deposit feeders, the bivalves are able to survive to maturity. Competition for resources (space and/or food) between adults of one bivalve species and juveniles of the other leads to a segregation of the two species along the tidal gradient. *Katelysia*, being less tolerant of desiccation, becomes confined to the lower sections of the beach.

iii. The other suspension feeding bivalve, *Wallucina*, is able to take advantage of low numbers of *Anapella* and *Katelysia* near a major beach ridge and *Wallucina* densities are highest there.

iv. The anemone, *Anthopleura*, uses large bivalves as a substrate and is

most abundant in the middle sections of the beach. Passive predation by *Anthopleura* acts to keep the numbers of deposit feeding gastropods low, thus minimising the effects of trophic amensalism in those regions. In the absence of *Anthopleura* at either end of the transect, relatively high numbers of deposit feeding gastropods lead to an exclusion of suspension feeding bivalves and hence to a reduction in community diversity.

v. The upper half of the beach appears to be most suitable for gastropods feeding on microalgae. Although the distributions of the algivorous gastropods suggested a degree of local competitive exclusion, this was not statistically significant.

vi. Interference competition between the algivorous gastropods and both the suspension feeding bivalves and the deposit feeding gastropods may be sufficient to influence the local distributions of those species.

vii. The gastropod *Nassarius* obtains its main food supply by scavenging dead, and preying on living, *Anapella* and *Katelysia*. The other carnivorous gastropod, *Cylichnina*, probably feeds on juvenile bivalves, and also on juvenile *Hydrococcus* and *Salinator*. Typically, the distribution of the predators is determined by the distribution of the prey and not *vice versa*. Apart from *Anthopleura*, therefore, predation appears to play a minor role in the maintenance of the community structure.

To summarise, the principal determining factor of the tidal flat community's structure appears to be trophic group amensalism, reinforced by the predation of *Anthopleura* on juvenile deposit feeders. The community structure, as described by diversity indices, can be explained in terms of Huston's (1979) dynamic equilibrium hypothesis, mediated by the trophic amensalism.

CHAPTER 1

GENERAL INTRODUCTION

The early development of quantitative ecology was strongly influenced by the spectacular successes of the physical sciences. Physicists have been able to define simple, fundamental laws that form the basis of very complex behaviour. Mathematics has played a dominant role in the description of physical processes and the laws are usually summarised by mathematical equations. Having identified the fundamental equations, it is possible to alter the parameters of those equations to predict the behaviour of physical processes under hypothetical conditions. The success of those predictions has been due to the constancy and predictability of the fundamental processes themselves. Probabilities and the associated uncertainties have only been introduced into the physical sciences through the theories of quantum mechanics.

In contrast, ecology has always been associated with the uncertainty that arises in the functioning of biotic systems, and also in the sampling of those systems. While the latter uncertainties can be minimised by judicious sampling, the former are intrinsic to the systems themselves, and cannot be influenced. Despite an acknowledgement of the unavoidable uncertainties inherent to biological processes, mathematical ecology developed on a foundation of attitudes and approaches more suited to the highly predictable physical systems. Mathematical ecologists have frequently sought simple, concise laws and equations which would purportedly lay the foundation for a biological equivalent of Newton's Laws of Gravitation, or Einstein's Laws of Relativity. This can perhaps best be illustrated by the following quotation of R. M. May, one of the leading figures in the development of mathematical ecology:

> "My background is in theoretical physics, and I am at least aware that my interests are liable to be animated too much by elegance and too little by commonsense" (May 1973 p. vi).

While the approach of the early mathematical ecologists can be criticised with the benefit of hindsight, it was an understandable approach, given the undeniable successes of the physical sciences that attracted so much attention at a time when ecology was still in its infancy. Nevertheless, I consider that the historical inertia of the simplistic, law-seeking approach has generated as much hinderance to our understanding of community (in particular) ecology as it has generated help.

Early community ecologists quite rightly recognised the importance of the constituent

populations. They attempted to reconstruct the behaviour of a given community from the behaviour of its component populations, in much the same way as physicists might reconstruct the behaviour of a solar system, for example, from a knowledge of the properties of the planets that make up that system. The uncertainty that makes ecology so different to physics prevents such reconstructions from being applied to anything but the simplest (usually laboratory) living communities or, alternatively, to mathematical community models. The important role of simple conceptual models has been stressed by Miller *et al* (1975) who suggested that the great benefit of such models lay in their stimulating effect on research. This is certainly true, particulary because of the ease of analysing model communities, when compared to the analysis of natural communities. While important insights (eg. Lotka 1925; Gause 1934; Birch 1948; Park 1948, 1954; Cole 1954; Vandermeer 1969; Neill 1975; Karlson and Jackson 1981) undoubtedly arise from such exercises, extrapolation to complex natural communities has rarely been possible.

Recently, the emphasis has shifted to detailed studies of natural communities and more biologically orientated interpretations of artificial systems. While these methods are not as elegant or definitive as the mathematical models, they are more realistic and therefore potentially more useful. The shift in emphasis has not been an entirely smooth transition. Adherents to mathematical modelling of populations and communities still argue for the merits of their approach. An example of such an argument is the different approach taken to the analysis of Nicholson's (1954) blowfly population data by scientists having biological and physical backgrounds. In a series of papers (Readshaw and Cuff 1980; Gurney *et al* 1980; Readshaw 1981; Gurney *et al* (1981), two opposing points of view were presented by members of the two schools. Readshaw (1981) considered that the conclusion reached by Gurney *et al* (1980), namely that Nicholson's (1954) data could be modelled by self-sustaining limit cycles, was esoteric, and approached a version of Hermann Hesse's (1972) "Glass Bead Game'. Readshaw (1981) argued that:

> "The gap between theoretical and applied ecology seems to be widening. Indeed it is difficult to escape the worrying conclusion that some theoreticians are playing a version of Hermann Hesse's *Das Glasperlen Spiel* or that they have little feeling for or understanding of biological problems".

The search for elegance is not of high priority in the present study. Elegance is sought in the analytical methods but unfortunately elegant analytical methods do not guarantee elegant findings. The complexity of natural communities inevitably leads to complex

analytical results and this complexity can only be reduced by the selective consideration of portions of the results. In the present study, for example, the multitude of species interactions within the study community is reduced by considering only consistently significant correlations (Chapters 5 and 6). This represents a compromise between too cursory and too detailed interpretations of the results. Unfortunately, the results of the analyses are still complex and, ideally, would themselves be subjected to a secondary analysis. The secondary analysis, however, demands hypotheses that can only be generated from the primary analysis, making for a vicious (and untidy) circle.

There is no escaping the difficulties in reconciling the results of empirical studies of communities with the predictions of models. The lack of empirical evidence supporting the findings of community models has been discussed by Foin and Jain (1977), who note that:

> "...in the absence of such data it is not surprising that the explanatory use of complex models should be regarded skeptically not only by other biologists and potential users but by many modelers as well" (Foin and Jain 1977).

The analysis of natural communities can be approached from two opposite directions. The first, and classical, approach is from 'below', from the level of the population. Knowledge of the behaviour of groups of individuals (or even single individuals) can be used to build up a composite picture of how a community should behave if two or more populations are combined. This process is usually intimately involved with mathematical population models. The opposite approach is from 'above', from the level of the whole community. Of necessity, this approach cannot be asociated with model building, except possibly in the final stages. Rather, it must involve decompositon processes. Thus, the approach from below uses mathematics to build up complexity, while the approach from above uses mathematics to decompose complexity. The former methods are frequently able to use deterministic equations to build non-random patterns while the latter use statistics to look for existing non-random patterns. The two approaches should meet somewhere near the middle and efforts have been made to achieve this (eg. Cramer and May 1972).

Prior to the last ten to fifteen years, community ecology was heavily biased towards the approach from below. Communities had been studied as whole entities (eg. Margalef 1963; Odum 1969) but the concerns were largely ones of community metabolism, rather than community dynamics (as distinct from trophic dynamics, *sensu* Odum and Odum 1956; Teal 1962). Foin and Jain (1977) outlined the development of community ecology

and suggested a paradigm for the analysis of communities and ecosystems. There are four steps to their paradigm:

1. descriptive analysis of those community level properties (eg. species composition, species diversity) considered relevant

2. generation of hypotheses about community structure and function

3. analysis of the populations involved in those community processes thought to be important

4. modelling of the population data to determine how well the structural and functional properties of the system can be understood.

This paradigm works from above, with recourse to population models only at the last stage of the analysis. This is the approach adopted in the present study, although time constraints prevented the fourth step from being achieved.

The reason why natural communities have not been studied as thoroughly as laboratory and model communities will always exist: natural communities are typically complex with unknown (in fact, effectively unknowable) levels of stochasticity emedded in their makeup. Ideally, the study of any community should involve at team of workers, each devoted to particular aspects. The community under scrutiny should be well known and easily sampled and monitored. The environmental conditions should also be easily monitored and as predictable as possible; the ideal habitat would be homogeneous and reasonably isolated from other habitats.

Some of these ideals could not even be approximated in the present study. The team, of course, was limited to one person, devoted to many aspects and hence completely covering none. In addition, Tasmania has no communities that could be considered well known and the initial part of any community study in Tasmania must be the determination of the makeup of that community. In an attempt to minimise these shortcomings as much as possible, the tidal flat mollusc community of a coastal lagoon in south-eastern Tasmania, Pipe Clay Lagoon, was selected for study. The tidal flat represents an extremely homogeneous habitat in comparison to many natural communities. The lagoon is open to the sea only through a narrow tidal channel and the sand flats are sheltered from most of the effects of storms. Fortunately, the mollusc community comprises relatively few species although their biology is virtually unknown in Tasmania.

Intertidal communities have played an inportant role in the development of our understanding of community structure and function. Early workers (Paine 1966, 1974; Dayton 1971, 1975; Connell 1972) concentrated on rocky shores but, more recently, the community structures of soft shores have attracted attention (Puttick 1977; Peterson

1977, 1979; Seapy and Kitting 1978). It is clear that there are considerable differences between the controlling influences of communities on rocky and soft shores and these have been described by Peterson (1979) and Dayton and Oliver (1980).

Although the soft substrates are easily sampled, soft-shore ecologists do not have the advantages with which rocky-shore ecologists are favoured. On rocky shores, the distributions of animals and plants are easily seen, without the need for sampling, and zonations and species interactions can be suggested by simple visual inspection. In contrast, few soft-substrate animals live on top of the sediments and samples must always be taken and sorted. Although animals may frequently be seen on top of soft substrates, the possibility that more animals are using the extra dimension demands that sampling.

The ease with which the community structure can be seen on rocky shores makes those communities amenable to manipulation experiments (eg. Paine 1974; Dayton 1975). As a rough figure, perhaps 10% of a rocky-shore ecologist's time might be spent on describing the community, with 90% available for manipulation experiments. On soft shores, however, the reverse is true. As will be seen in the following chapters, the 'simple' description of the Pipe Clay Lagoon community required well over 2000 hours of sorting; even then the community could only be sampled quarterly and only a portion of the community could be considered. A full listing of the raw survey data, together with the magnetic tape data base, has been lodged with this thesis in the University of Tasmania Library. Future workers may be able to build on the description of the community and hopefully improve the ratio of experimental to survey work. Pipe Clay Lagoon represents an ideal site for a team research effort.

In following the paradigm of Foin and Jain (1977), the initial stage of this project involved a major sampling program, described in Chapter 2, from which the makeup of the mollusc community could be determined. The sampling also provided demographic information which shed light on the reproductive biologies of the species; these findings are described in Chapter 3. Chapter 4 examines the changes in the structure and diversity of the community along the tidal gradient, and through the change of seasons. On the basis of those observations, a working hypothesis for the control of the community structure is proposed. Chapter 4 represents a pivotal chapter between the description of the community, the generation of hypotheses and the later testing of those hypotheses.

The hypothesis testing is conducted in three stages. Firstly, Chapter 5 examines the correlation between the species distributions and various physical paramters, and also between the species distributions themselves, along the tidal gradient. In Chapter 6, the species correlations are examined at a much smaller scale, in an attempt to test the

conclusions of Chapter 5. Finally, caging manipulation experiments, described in Chapter 7, are used to further test the conclusions drawn from the previous chapters. Thus, Chapters 2 to 6 are based on survey work and Chapter 7 is based on experimental work.

I believe that the approach to the analysis of the survey data adopted in this study has a great deal of potential. In Chapter 5, a spatial equivalent of time series analysis is used to examine species relationships along the tidal gradient. The series analysis shifts two given series relative to each other, firstly in one direction and then in the other; the shift can be made for a variety of lags. Potentially, this method of analysis can detect the correlations between the density of one species and the density of another species some distance up or down the transect. This allows an examination of the role that species interacitons have in determining the zonation patterns of species on unidirectional environmental gradients. This approach does not appear to have been taken before.

As a two-dimensional cororally to the series analysis of Chapter 5, Chapter 6 uses the methods of spatial auto- and cross-correlation analysis to examine species correlations within a grid of contiguous quadrats. The methods adopted detect interactions between species at various distances apart, within the sampling grid. Thus, Chapter 5 looks at relationships in one dimension, over relatively large distances, and Chapter 6 looks at relationships in two dimensions, over considerably smaller distances.

As will be seen, the existence of a master plan for the analysis did not inexorably lead to clear insights into the structural dynamics of the Pipe Clay Lagoon mollusc community. Many of the findings are ambiguous, or at best tentative. This is undoubtedly due to the time constraints placed on the sampling program. A more intensive and extensive sampling program would be required to increase the fidelity of the analysis and hence decrease the tentativeness of the conclusions. Nevertheless, the methods adopted in this study are recomended and, with increased manpower, resources and time, should prove to be useful additions to the analysis of community dynamics.

It is essential to recognise from the outset the approach adopted in the following pages. This study is <u>not</u> an examination of the biology of the mollusc species of Pipe Clay Lagoon. In fact, very little biological data was collected. The likely biology of the species, as determined from other studies of the same or closely related species, is used only to put the findings of the present work into perspective. This study examines the community structure in terms of an entity exhibiting temporal and spatial behaviour and the approach is diametrically opposite to the usual biological approach. Little direct biological information was sought and little will be provided in the following pages. To expect otherwise would be to view the study from upside down. Numerous biological studies are suggested by this work and could be designed to test the hypotheses developed. The two approaches, originating from opposite ends of a spectrum, should meet somewhere near the middle.

CHAPTER 2

DESCRIPTION OF SURVEY METHODS, PHYSICAL CHARACTERISTICS OF THE TIDAL-FLAT AND INTRODUCTION TO THE FAUNA

2.1 Introduction

This study is based on a temporal and spatial survey of the northern tidal flat of Pipe Clay Lagoon, near Cremorne on the South Arm Peninsula in south-eastern Tasmania. The lagoon covers an area of approximately 8 km^2 and is open to Frederick Henry Bay through a narrow tidal channel; extensive areas of tidal flats are exposed at low tide (Fig. 2.1). There is little freshwater runoff into the lagoon apart from rare flood waters entering from the *Salicornia* marshes around the perimeter. A preliminary survey indicated that the northern tidal flat is the richest, in terms of both faunal abundance and diversity; this is probably largely due to the deposition of water-borne nutrients entering through the tidal channel (the greater abundance of organic matter in the substrate is sufficient to produce a darker colouration, relative to the southern flats). The faunal richness led to the selection of the northern flat as the study area.

There has been only one previous study of the intertidal zone of Pipe Clay Lagoon (Guiler 1950). Guiler conducted a general survey of the lagoon and also included a more detailed examination of a transect extending down the intertidal gradient on the northern shore. The present study is based on transects between EHWS (extreme high water spring) and MLW (mean low water) laid in approximately the same position as Guiler's transect.

The structural dynamics of any community (in this work, the term 'community' is defined to be a faunal assemblage existing within a prescribed area) will be determined, both directly and indirectly, by interactions within and between abiotic and biotic factors. Obviously some of these factors will be more important than others, but it is not possible to determine factor rankings *a priori* when a community is being studied for virtually the first time. It is neccessary, therefore, to make selections of likely candidates for the role of controlling agents, based on the available information from other studies.

The distribution of soft-substrate intertidal organisms has been linked with many factors, including exposure and beach slope, sediment grain size, organic content of the

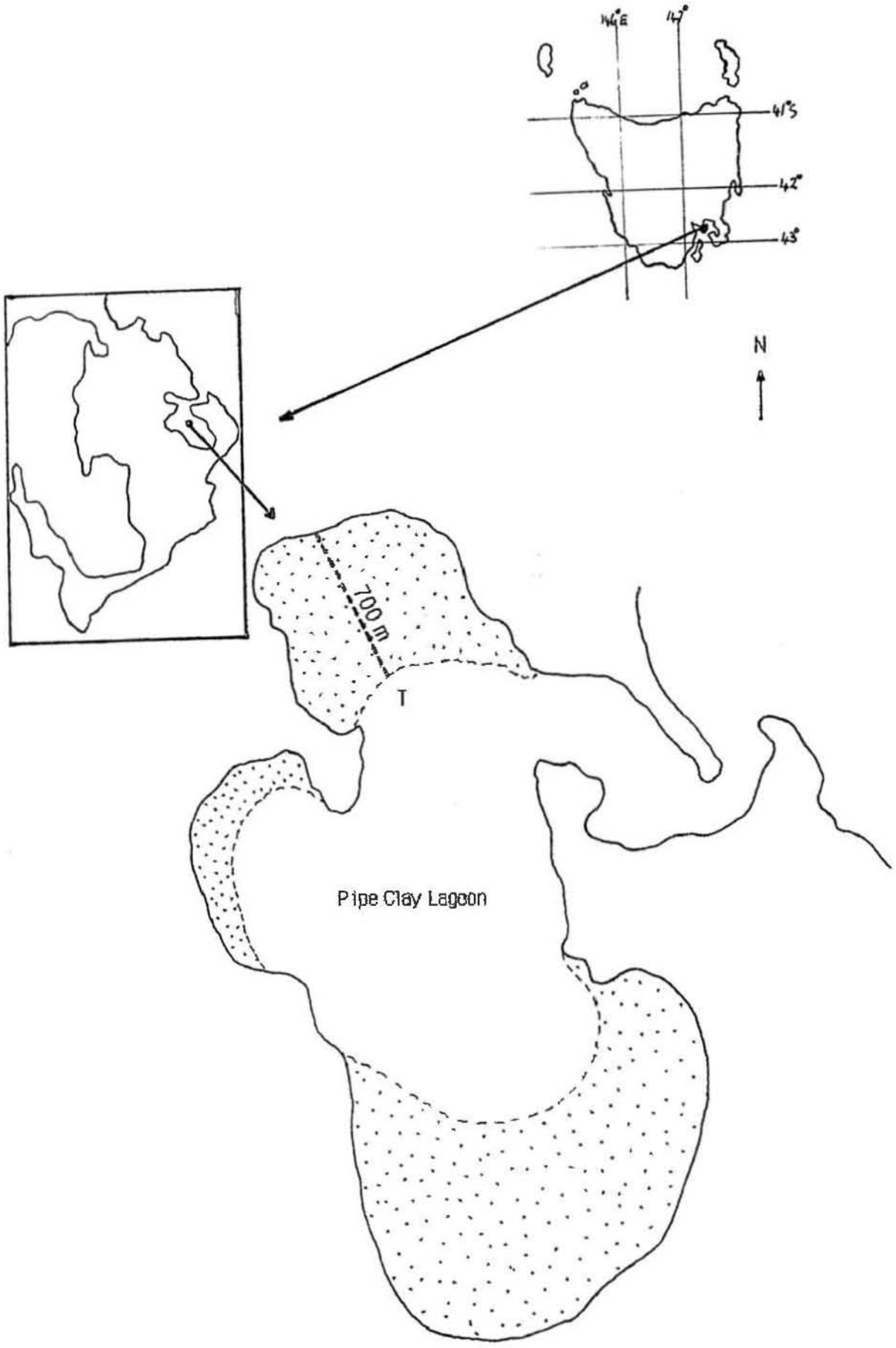


Fig. 2.1 Location of study site, on the South Arm Peninsula in southeastern Tasmania. Stippled areas mark tidal flats; dotted line identifies the position of the 700 m sampling transect.

substrate, sediment moisture, water-borne nutrients and small and large scale disturbances (McLachlan 1983). These factors do not necessarily act in isolation and often show complex interelationships. Bolter *et al* (1981) measured the correlations among a large number of physical, chemical, planktological and microbial parameters in shallow (brackish) waters. They found a large variety of relationships, with the central parameters being salinity, nitrite, particulate organic carbon and nitrogen, free dissolved glucose and ribose, bacterial biomass, filamentous cells and biological oxygen demand.

The relationships between physico-chemical parameters and organisms are frequently bilateral processes. Deposit feeders, for example, may reduce the organic content of the substrate (Tsuchiya and Kurihara 1980). Biogenic processes of bacteria, unicellular plants and invertebrates can affect the stability of sediments (Grant *et al* 1982) while animal tubes and seagrasses may exert effects on the near-bed water flow (Eckman 1983).

Such effects of organisms on the physical or chemical characteristics of the substrate can mediate relationships between different species. Thus, Weinberg and Whitlach (1983) have shown that the activity of polychaete worms (*Clymenella torquata*) transports nutrient rich interstitial water out into the overlying water, stimulating microfloral populations and hence improving clam (*Gemma gemma*) growth. They suggested that those activities may be a contributing factor to the common associations between the two species.

Commonly, the activities of organisms appear to exert negative effects on other species. Rhoads and Young (1970, 1971) formulated the 'trophic group amensalism' hypothesis, suggesting that bioturbation by deposit feeders leads to the exclusion of suspension feeders. They noted, however, that such sediment destabilisation tends to be confined to deep, subtidal bottoms; shallow and intertidal sediments are often stabilised by seagrasses, diatoms, algal mats and animal tubes.

The relationships between the physico-chemical parameters of a marine substrate and its biota are very complex. This study is not concerned with examining the mechanisms of abiotic and biotic interactions on the Pipe Clay Lagoon tidal flat. Rather, it is aimed at describing the consequences of those interactions. To this end, correlations between the distribution of species and the major physical parameters and also between the distributions of different species were sought.

The selected physical features include the beach profile, minimum-maximum temperatures along that profile, sediment characteristics, organic content of the substrate and the abundance of algal mats and polychaete worm tubes.

Short and Wright (1983) identified three basic types of beach profiles: 'dissipative', 'reflective' and 'intermediate'; the intermediate group is further subdivided into four states, making a total of six states. Dissipative beaches are formed through exposure to high wave action and are characterised a wide, low profile built up of fine sands. Reflective beaches are produced in areas of low wave action and have steep faces and coarse sediments. Intermediate beach types have obvious longshore variability and often have an offshore bar and trough.

There is a general, negative correlation between grain size and beach slope, for given wave action (Flemming and Fricke 1983). Thus, steeper sloping beaches tend to comprise coarser grains. Sediment size may vary wih depth and season. Amspoker and McIntyre (1978), for example, detected an increase in grain size with depth and observed that late winter sediments were coarser than summer/autumn sediments. Algal mats and polychaete worm tubes may act to stabilise the substrate (Ginsburg and Lowenstam 1958; Fager 1964; Myers 1972; Aller and Dodge 1974).

There may also be relationships between grain size and organic content, due to differential trapping of particulate organic matter. Pugh *et al* (1974) noted that finer sands trap more organic matter and that seasonal variation of organic content was greater on a fine sand beach than on a coarse sand beach. Usually, the distribution of organic carbon shows a strong, positive correlation with the distribution of fine sediment particles (Tietjen 1977; Tsuchiya and Kurihara 1980).

Temperature fluctuations in an intertidal area will be influenced by a complex of factors, both terrestrial and marine. Generally it would be expected that inundation would act as a moderating influence on temperature extremes. Mean temperatures, however, need not be determined by aerial exposure. Wilson (1983), for example, showed that although hourly mean temperatures differed markedly from month to month at the mean tide level, they were similar for different depths during the same month.

The combination of the above abiotic factors and also interactions within and between the species present in the intertidal community could be expected to account for much of the dynamic structure of that community. The expression of those interactions will be examined in subsequent chapters. The following section describes the physical characteristics of the Pipe Clay Lagoon tidal-flat and introduces the species representing the tidal-flat community.

2.2 Methods

2.2.1 Introduction

The intertidal zone is characterised by a strong environmental gradient - tidal exposure. It is therefore possible to identify both 'vertical' (along the gradient) and 'horizontal' (across the gradient) components to the system.

Horizontal patterns of the mollusc assemblage could be expected to be largely independent of the tidal regime and much of the non-random structure of the populations may be attributable to interactions within and between the populations. Obviously there may be other determining factors not accounted for but this 'noise' component must be disregarded (although not forgotten) after defining the physical and biotic components of the assemblage.

The vertical patterns of the assemblage will be influenced by both the horizontal biotic interactions and the environmental gradient.

The sampling program was designed to allow analysis by statistical techniques concerned with identifying biotic interactions in one (vertical) or two (horizontal) dimensions. The methods of analysis in the following chapters (except Chapter 7) are based on the observed abundances of organisms in located quadrats.

The sampling can be divided into two distinct areas. The vertically based sampling involved 'distribution transects' while the horizontally based sampling involved 'dispersion transects'. These terms will be used throughout the subsequent chapters.

2.2.2 Distribution transects

A transect path extending 700 m along the tidal gradient from EHWS to MLW was marked permanently at 100 m intervals with wooden stakes driven into the substrate. All transects were taken within 10 m either side of this path. Single quadrat samples were taken every 20 m along this path, from 0 m (EHWS) to 700 m (MLW), making a total of 36 quadrats for each distribution transect. Positions on the beach will be identified in this manner by their horizontal distance from EHWS. Successive transects were taken on alternate sides, and 5 m and 10 m from the transect path.

Distribution transects were taken in each season, with the sampling dates being 200381 (autumn), 270681 (winter), 290981 (spring), 291281 (summer) and 310382 (autumn). Here, 200381 represents the 20 th of March, 1981, and so on. Throughout this work the dates and seasons are identified in this way.

Each quadrat covered an area of 0.25m x 0.25 m and the substrate was removed to the depth of the anoxic layer (typically c. 5 cm). If the quadrat contained a feeding aggregation of *Nassarius* , it was taken again; this was the only selectivity in the local

placing of the quadrats.

The sampling commenced when the water level was approaching the midpoint of the tidal ebb. Each quadrat sample was transferred to a capped plastic container. The sampling typically took at total of 2 - 3 hrs. All samples were returned to - 10 ^{0}C storage within about 4 hrs, following the final sample.

Immediately following the sample collections, the beach profile was surveyed with a theodolite. The surveying commenced at the 700 m mark of the transect and moved in 20 m intervals up the beach to EHWS, identifying the vertical positions each quadrat.

For sorting, the frozen samples were thawed as needed and sieved through a 500 µm brass screen using warm, running, fresh water. The sediment was collected and refrozen for later analysis. The remaining fraction was washed into a white, plastic sorting tray and manually sorted with a pair of fine forceps.

All occupied mollusc shells, including the spat, were extracted, together with any anemones. The anenomes were included because of obvious relationships with a number of the molluscs. Each quadrat typically required 8 hrs sorting, making a total of approximately 290 hrs for each distribution transect.

The animals were measured to the nearest millimeter using a pair of vernier callipers. For the bivalves (and limpets) the measurement was taken across the width of the shell, for the gastropods (excluding limpets) along the height, and for the anenomes across the basal disc. Each animal was assigned to 1 mm size classes. Animals in the smallest size class, containing 0 - 1 mm individuals, are referred to as '0 mm' animals; those in the 1 - 2 mm class as '1 mm' animals and so on. The convention will be followed throughout this work.

Following the removal of the biota, the shell debris, algae and polychaete worm tubes were separated and weighed.

With each quadrat, the sediment passing through the 500 µm sieve was stored at - 10 ^{0}C until analysed. After thawing, approximately 50 g (wet weight) was placed in a drying oven at 70 ^{0}C for 24 hrs. A small weighed fraction (c. 10 g) of the dried sample was then placed in a muffle furnace at 475 ^{0}C (Byers *et al* 1978) for 24 hrs. The percent weight loss of that fraction was recorded. The remaining c. 40 g was dispersed with 6.2 g/l sodium polymetaphosphate $(NaPO_3)_6$ according to the methods of Buchanan and Kain (1971). After soaking overnight, the dispersed sediment was dried for 24 hrs before sieving through a series (250, 125 and 63 µm) of brass sieves. The proportion of sediment passing through each sieve was recorded.

The above treatments of the distribution transect quadrats resulted in each quadrat

being characterised by:

1. the horizontal distance down the transect from EHWS
2. the vertical height below EHWS
3. the weight of shell debris > 500 µm
4. the sediment fractions passing through 250, 125 and 63 µm.
5. the organic content, as measured by the % ignition loss
6. the wet weight of the algal mats
7. the wet weight of the polychaete worm tubes

and 8. the number and size of all molluscs and anenomes

2.2.3 The dispersion transects

The dispersion transects were taken along the same path as the distribution transects. Single grid samples were taken at 100 m intervals from 100 m to 700 m below EHWS, making a total of 7 grids for each dispersion transect. Sampling was conducted on the day following the distribution transect sampling, but for convenience they will be referred to by the same dates: 200381, 270681, 290981 and 291281. No 310382 dispersion transect was taken. Successive transects were taken on alternate sides, and 2.5 m and 7.5 m from the transect path.

Each grid covered an area of 0.5 m x 0.5 m, divided into 8 x 8 equal cells and the substrate was removed from each cell to the depth of the anoxic layer. As before, the grids containing *Nassarius* feeding aggregations were retaken. Each cell sample was transferred to a capped plastic container and returned to -10 ^{0}C storage until required for sorting. Again, the sampling typically took at total of 2 - 3 hrs and all samples were returned to -10 ^{0}C storage within about 4 hrs, following the final sample.

At each of the 100 m marker stakes, minimum/maximum thermometers were set up for the duration of the sampling year, buried in the top 2 cm of the substrate. Minimum and maximum temperatures were recorded at 2 - 4 week intervals.

In the laboratory the fauna was removed samples and classified as before. The shell debris, worm tubes, algal mats and sediment characteristics were not considered for the dispersion transects.

Each sample typically required 30 min to sort, making a total of approximately 225 hrs for a complete transect.

Each season's distribution and dispersion transects therefore required at total of approximately 515 hrs of sorting.

2.3 Results

2.3.1 Physical parameters

2.3.1.1 Beach profile

Figure 2.2 shows the profile of the Pipe Clay Lagoon tidal flat as determined on each of the distribution transect sampling dates. There is little variation between seasons, although the winter (270681) profile shows evidence of excavation between 400 m and 500 m and a steeper 500 m to 700 m slope.

A number of features can be identified in each season:

1. a comparatively steep upper beach slope that drops approximately 20 cm over the upper 150 m
2. an approximately horizontal zone extending from 150 m to 250 m
3. a small ridge rising 2-3 cm between 250 m and 350 m
4. a 3-4 cm trough between 360 m and 420 m
5. a high ridge rising approximately 10 cm from the trough (7-8 cm above zone 2) between 420 m and 500 m before falling symmetrically to c. 600 m
6. a continuation of the fall to 700 m, making for an overall lower beach slope fall of 20-25 cm from 500 m to 700 m.

2.3.1.2 Shell debris

The distribution of shell debris along the transects (Fig. 2.3) shows correlations with the above features. The upper slope (zone 1) is characterised by abundant shell debris. There is also evidence of debris build up above each of the two ridges (zones 3 and 5) and also against the lower beach slope of zone 6. Overall, shell debris appears to be more abundant in autumn/winter than in spring/summer.

2.3.1.3 Sediment sorting characteristics

In contrast to the patterns of distribution of shell debris, there is little significant trend in the sediment sorting characteristics in any season (Table 2.1). Typically, the mean phi value for the sediment lies between 2.48 and 2.50 while the sorting indices are close to 0.40 (well sorted medium to fine sand: Gray 1981).

There are trends within the individual size fractions, however (Fig. 2.4). Particles less than 63 µm show wide variability in both the spatial and temporal dimensions. Despite this, two loosely defined, broad peaks can be discerned centred near 200 m and 500 m respectively. Two peaks are also present in the distribution of 63-125 µm particles but these are more sharply defined and are displaced with respect to the above peaks. Thus, the first peak lies near the 250 m mark and the second

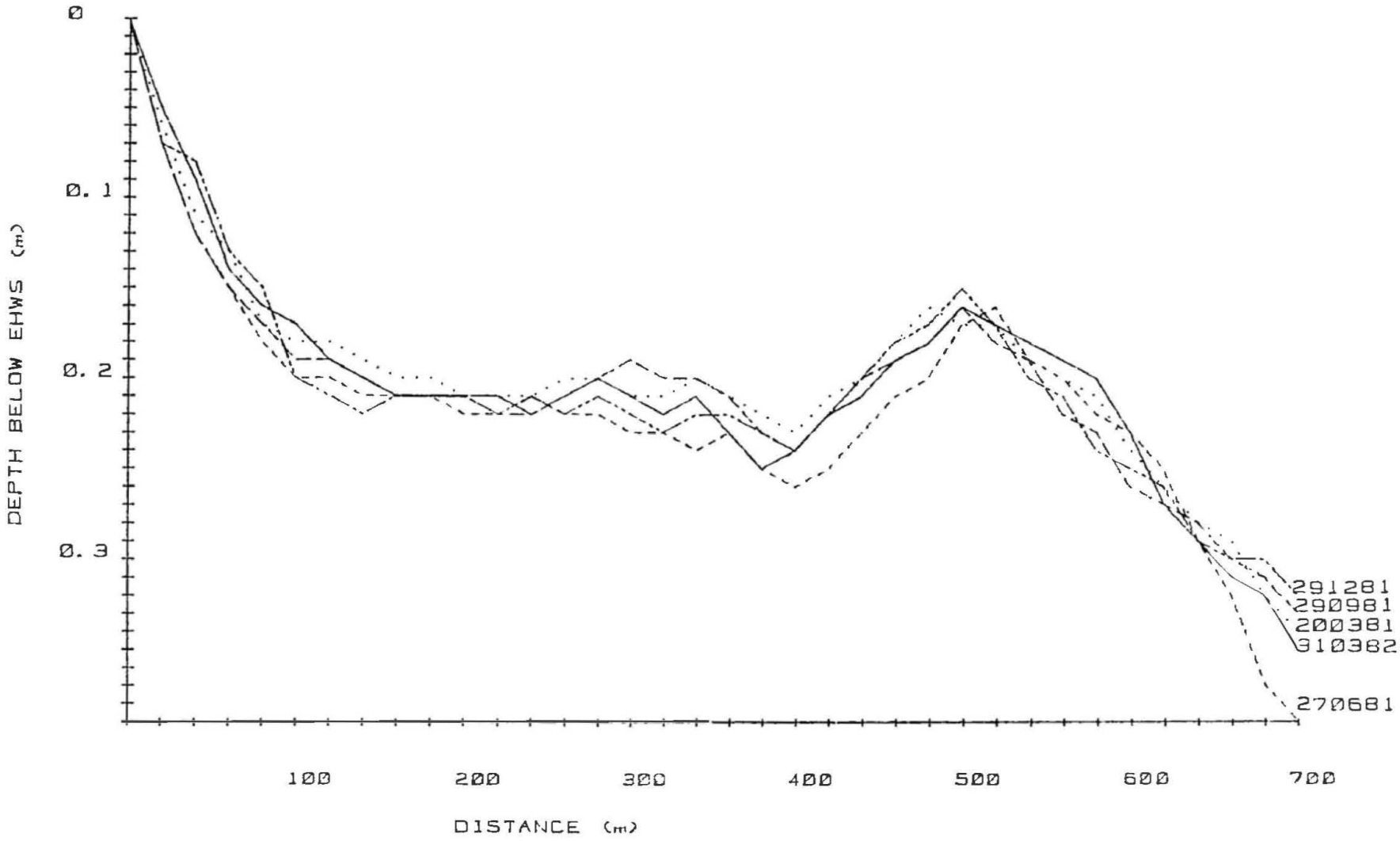


Fig. 2.2 Beach profile on the transect sampling dates. Distance measured from EHWS.

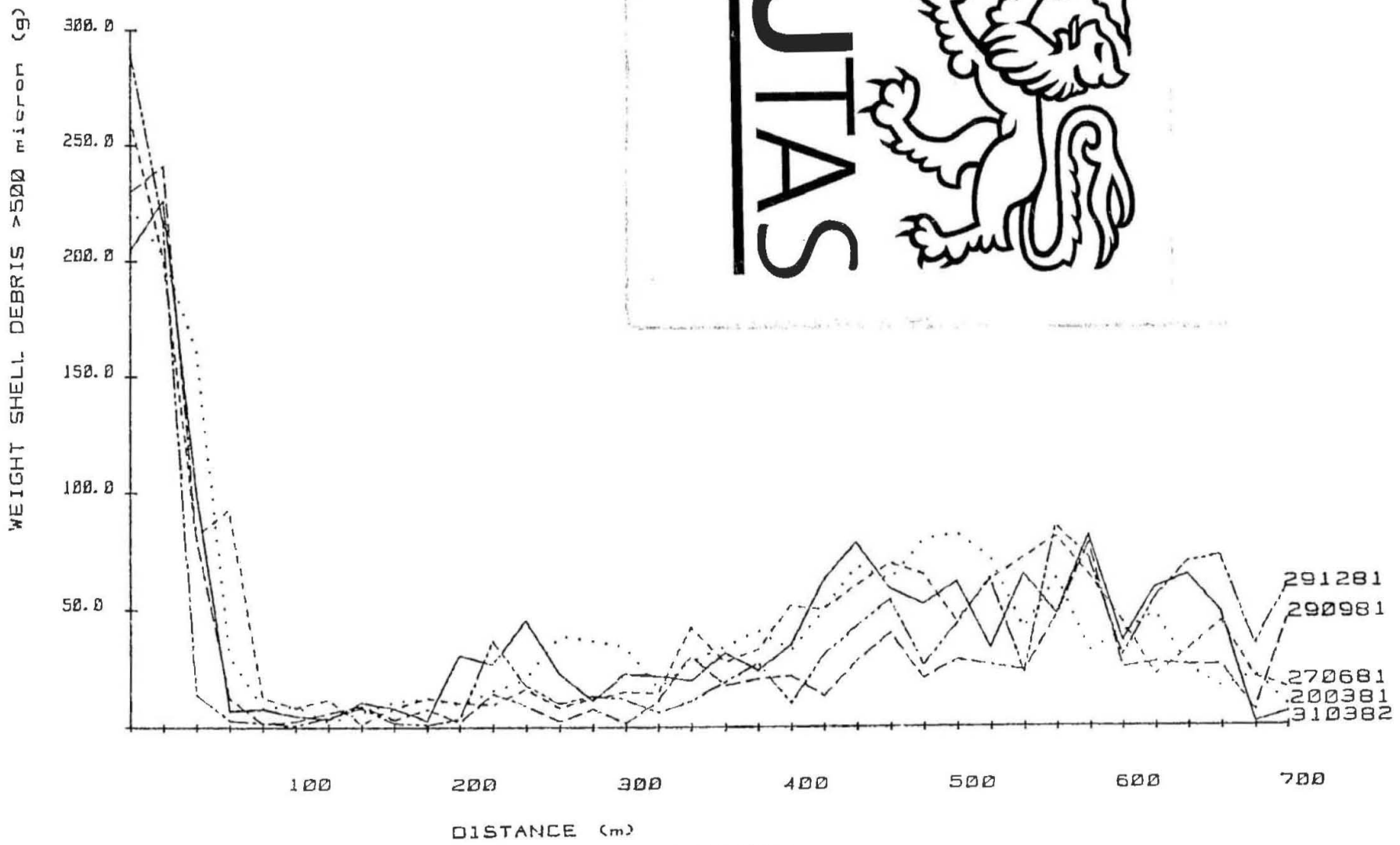


Fig. 2.3 Distribution of shell debris on the transect sampling dates.

Table 2.1: Sediment sorting characteristics along seasonal distribution transects.

Distance is horizontal distance from EHWS in metres.

DISTANCE (m)	MEAN SIZE, SORTING COEFFICIENT (phi units)				
	200381	270681	290981	291281	310382
0	2.51, 0.43	2.49, 0.39	2.48, 0.41	2.43, 0.41	2.48, 0.41
20	2.49, 0.41	2.49, 0.40	2.48, 0.40	2.47, 0.41	2.50, 0.43
40	2.50, 0.42	2.49, 0.39	2.48, 0.41	2.50, 0.39	2.53, 0.41
60	2.50, 0.41	2.50, 0.41	2.48, 0.40	2.49, 0.39	2.46, 0.41
80	2.48, 0.41	2.46, 0.42	2.49, 0.41	2.48, 0.40	2.48, 0.41
100	2.49, 0.41	2.47, 0.37	2.49, 0.39	2.50, 0.41	2.49, 0.40
120	2.49, 0.38	2.47, 0.38	2.48, 0.39	2.50, 0.40	2.49, 0.39
140	2.48, 0.39	2.48, 0.39	2.48, 0.39	2.47, 0.39	2.49, 0.39
160	2.48, 0.40	2.48, 0.39	2.48, 0.39	2.50, 0.40	2.48, 0.41
180	2.48, 0.40	2.49, 0.38	2.48, 0.39	2.47, 0.39	2.46, 0.41
200	2.48, 0.41	2.47, 0.40	2.48, 0.40	2.49, 0.38	2.46, 0.40
220	2.47, 0.40	2.47, 0.38	2.47, 0.39	2.44, 0.42	2.47, 0.40
240	2.47, 0.39	2.44, 0.41	2.45, 0.41	2.46, 0.39	2.45, 0.40
260	2.48, 0.40	2.42, 0.46	2.46, 0.41	2.45, 0.41	2.46, 0.41
280	2.45, 0.40	2.46, 0.39	2.48, 0.39	2.49, 0.40	2.46, 0.42
300	2.45, 0.40	2.46, 0.40	2.48, 0.40	2.48, 0.38	2.47, 0.40
320	2.47, 0.40	2.48, 0.39	2.48, 0.39	2.48, 0.38	2.46, 0.39
340	2.47, 0.39	2.48, 0.42	2.48, 0.40	2.51, 0.40	2.47, 0.39
360	2.49, 0.39	2.49, 0.38	2.49, 0.40	2.49, 0.38	2.48, 0.40
380	2.48, 0.39	2.50, 0.37	2.49, 0.38	2.49, 0.38	2.47, 0.39
400	2.49, 0.40	2.48, 0.38	2.48, 0.39	2.48, 0.39	2.49, 0.38
420	2.49, 0.39	2.48, 0.38	2.48, 0.38	2.47, 0.40	2.49, 0.39
440	2.49, 0.39	2.51, 0.39	2.48, 0.39	2.48, 0.39	2.47, 0.39
460	2.50, 0.39	2.47, 0.39	2.48, 0.39	2.49, 0.38	2.48, 0.40
480	2.49, 0.39	2.47, 0.40	2.48, 0.40	2.47, 0.40	2.47, 0.39
500	2.48, 0.39	2.49, 0.39	2.48, 0.38	2.48, 0.39	2.48, 0.40
520	2.48, 0.39	2.48, 0.39	2.47, 0.38	2.48, 0.39	2.48, 0.39
540	2.48, 0.40	2.49, 0.38	2.49, 0.39	2.49, 0.38	2.50, 0.38
560	2.49, 0.39	2.49, 0.37	2.49, 0.38	2.50, 0.38	2.49, 0.39
580	2.48, 0.40	2.50, 0.38	2.49, 0.38	2.50, 0.38	2.49, 0.39
600	2.48, 0.40	2.49, 0.38	2.49, 0.39	2.49, 0.37	2.50, 0.40
620	2.49, 0.39	2.49, 0.39	2.50, 0.39	2.50, 0.39	2.49, 0.40
640	2.49, 0.39	2.50, 0.38	2.50, 0.39	2.49, 0.40	2.50, 0.39
660	2.49, 0.40	2.50, 0.39	2.52, 0.39	2.50, 0.38	2.51, 0.38
680	2.50, 0.39	2.49, 0.39	2.50, 0.38	2.49, 0.39	2.52, 0.39
700	2.50, 0.39	2.52, 0.38	2.51, 0.38	2.51, 0.39	2.52, 0.38

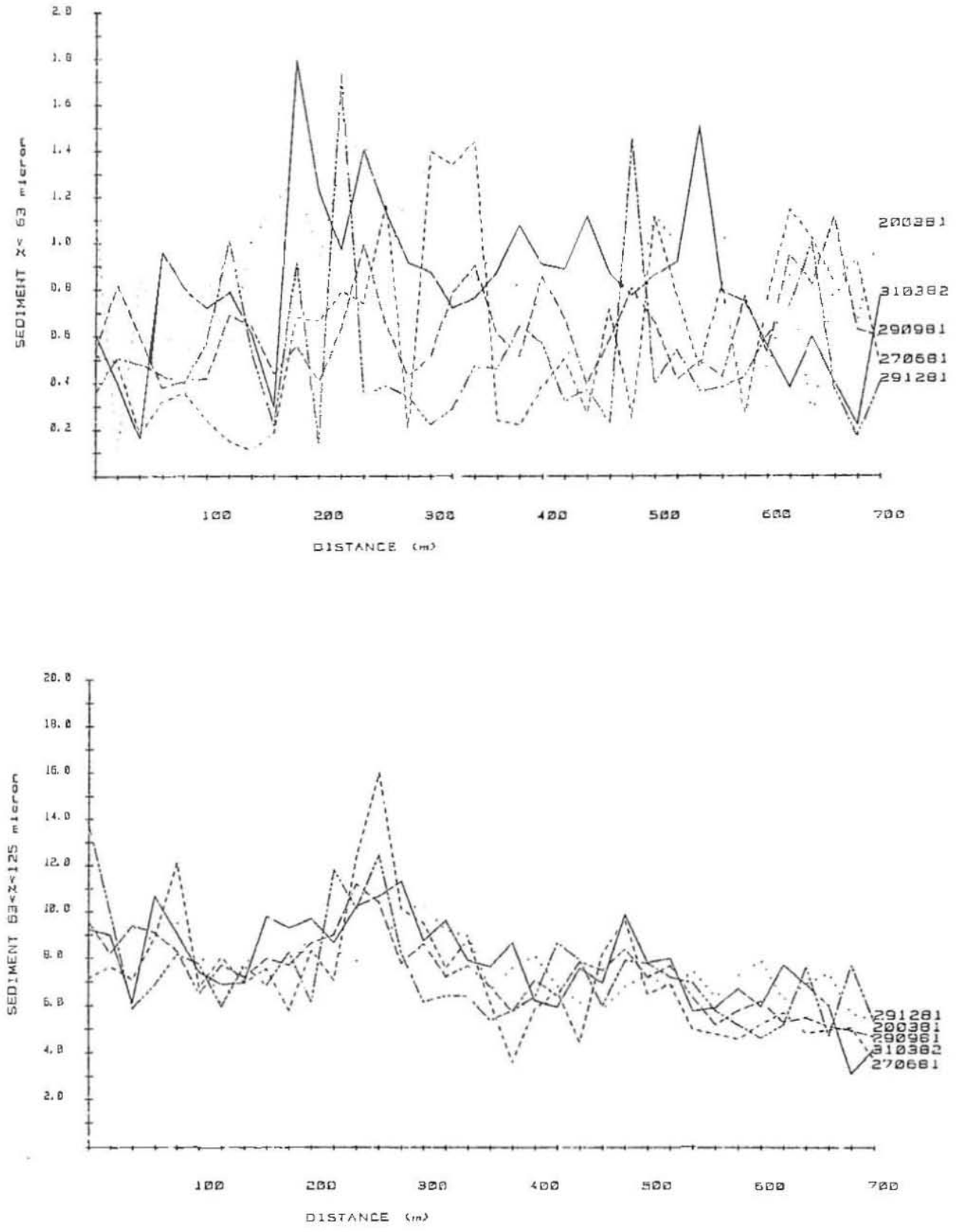
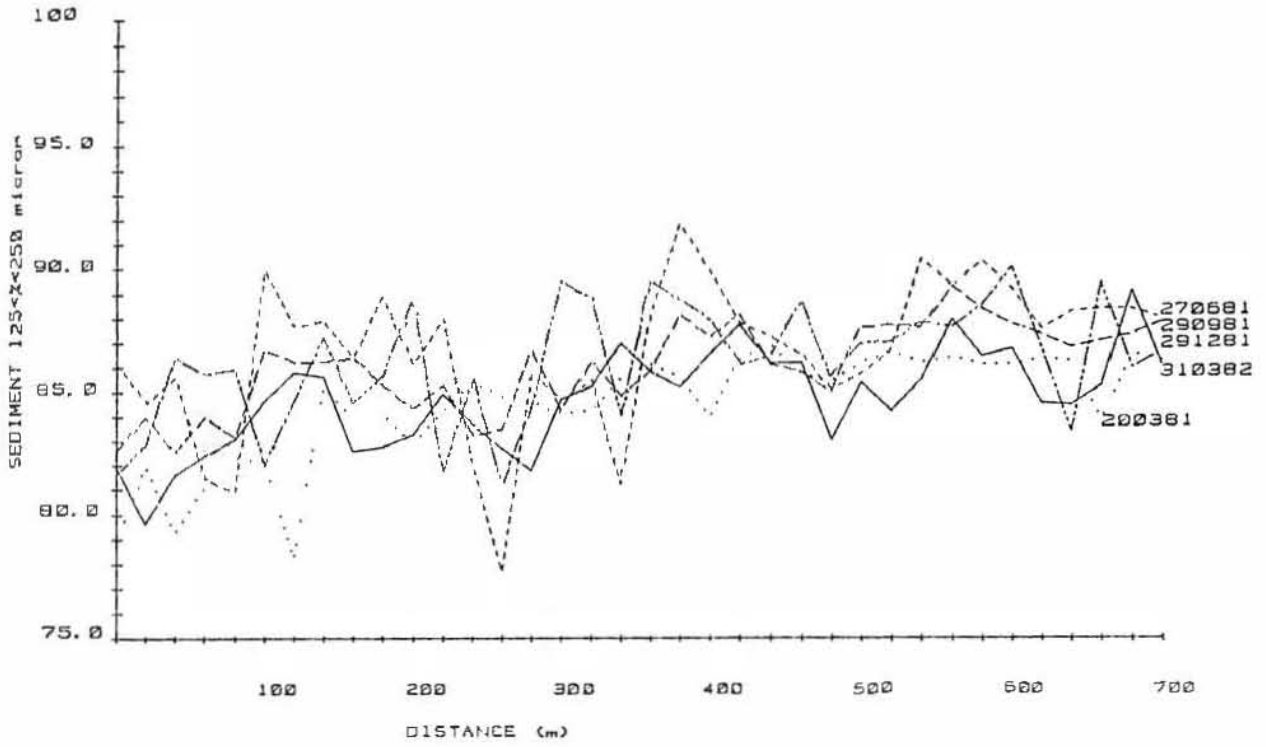


Fig. 2.4 Percent representation of sediment fractions on transect sampling dates.



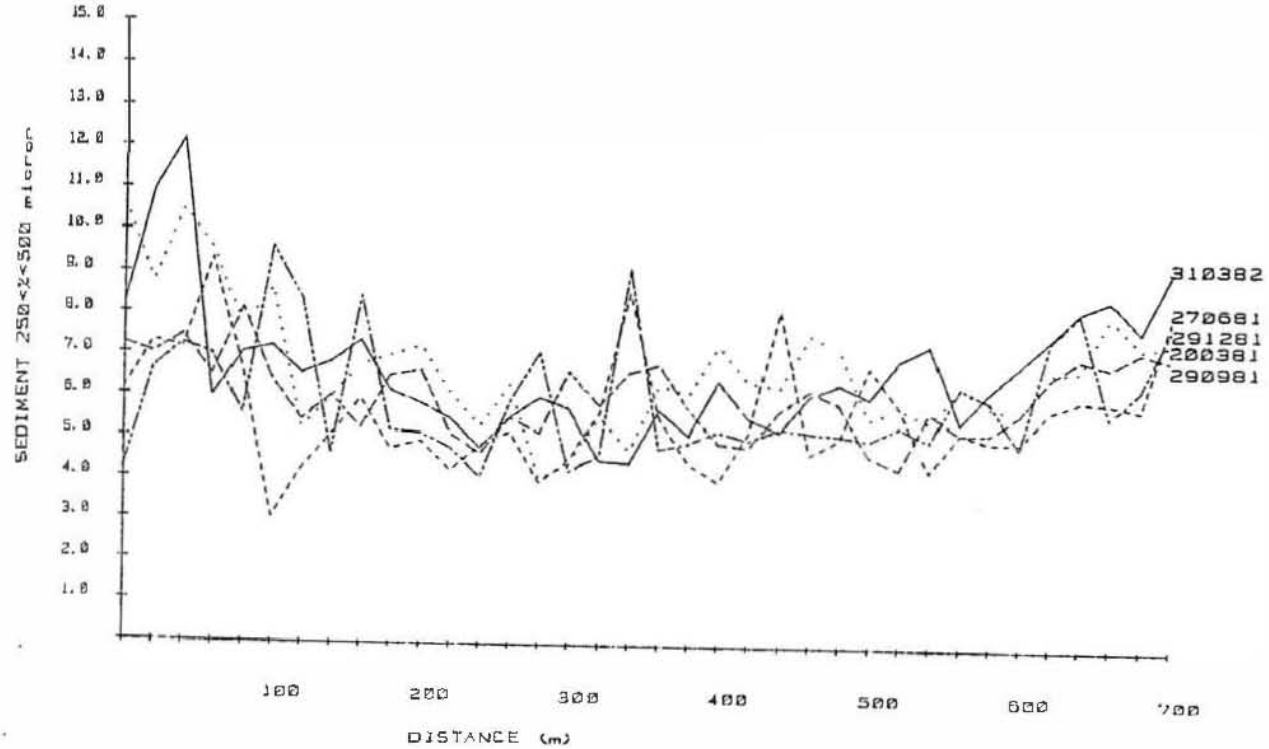


Fig. 2.4 (continued)

near the 480 m mark; there is comparatively little seasonal variation. Among the 125-250 μm particles (the most common sizing), there is a general trend for an increasing proportional representation with horizontal distance down the beach. Where the previous size fraction showed peaks, this fraction shows troughs. The coarsest particles are most abundant on the upper and lower beach slopes (beach profile zones 1 and 6). Towards the centre of the beach this fractions representation diminishes, apart from a small peak near the 350 m mark.

Although there is no apparent mean size sorting gradient with respect to position on the beach profile, each season does show a region of deviation from the typical mean phi value, with phi values there lying between 2.44 and 2.46. The position of this region remains relatively constant from season to season: on 200381 it lies approximately between 280 m and 300 m, on 270681 between 240 m and 300 m, on 290981 between 240 m and 260 m, on 291281 between 220 m and 260 m and on 310382 between 240 m and 280 m.

2.3.1.4 Organic content

The changes in organic content of the sediment (Fig. 2.5) along the transects show trends similar to those of the beach profile. The upper beach slope (zone 1) is characterised by a high organic content which falls to a steady value (c. 0.5%) in zone 2. The first ridge of the beach (zone 3) shows a peak in organic content before a drop in the region of the zone 4 trough. There is a broader, lower peak in organic content associated with the second beach ridge and the lower beach slope (zones 5 and 6).

Overall, organic content appears to be highest on 200381 but the relatively low values on 310382 suggest this is not a consistent seasonal effect.

2.3.1.5 Algal mats

The *Synechococcus / Oscillatoria* algal mats are generally restricted to between 50 m and 200 m, although on 200381 they extend down to about 400 m (Fig. 2.6). In each season there is a rapid rise in abundance from c. 50 m to a peak between 80 m and 100 m. On 200382 and 291281 there is a secondary peak between 260 m and 340 m. The mats are most abundant on 200381, suggesting a (late) summer bloom followed by a decrease over winter and spring. The low abundance on 310382 indicates that the algal bloom is not a consistent seasonal occurrence.

2.3.1.6 Polychaete worm tubes

The algal mats and polychaete worm tubes appear to be approximately mutually exclusive. The worm tubes are restricted to below c. 150 m where they increase to a peak before a general reduction through to 700 m (Fig. 2.7). On 200381 there is a

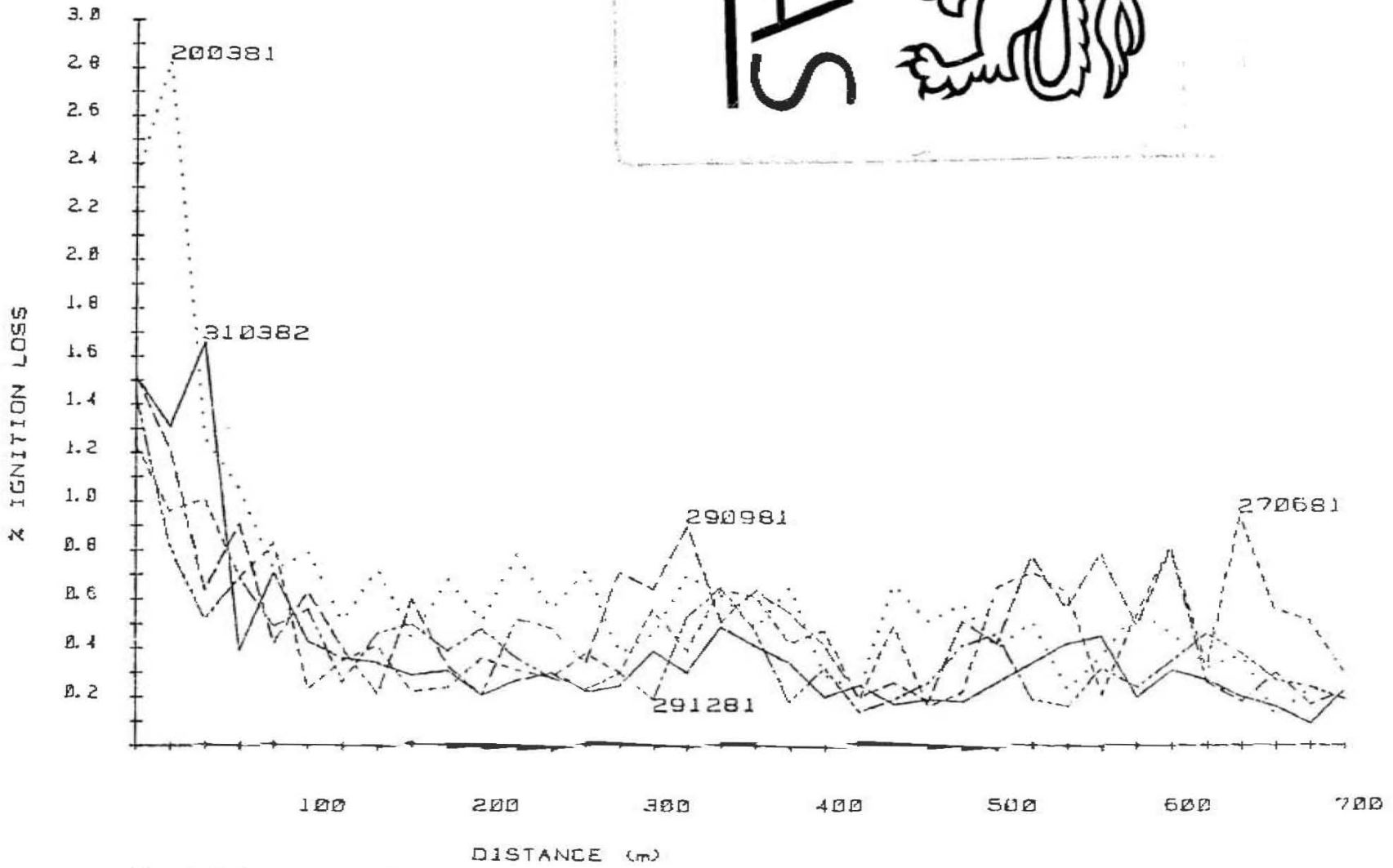


Fig. 2.5 Organic content, measured as percent ignition loss, of substrate on transect sampling dates.

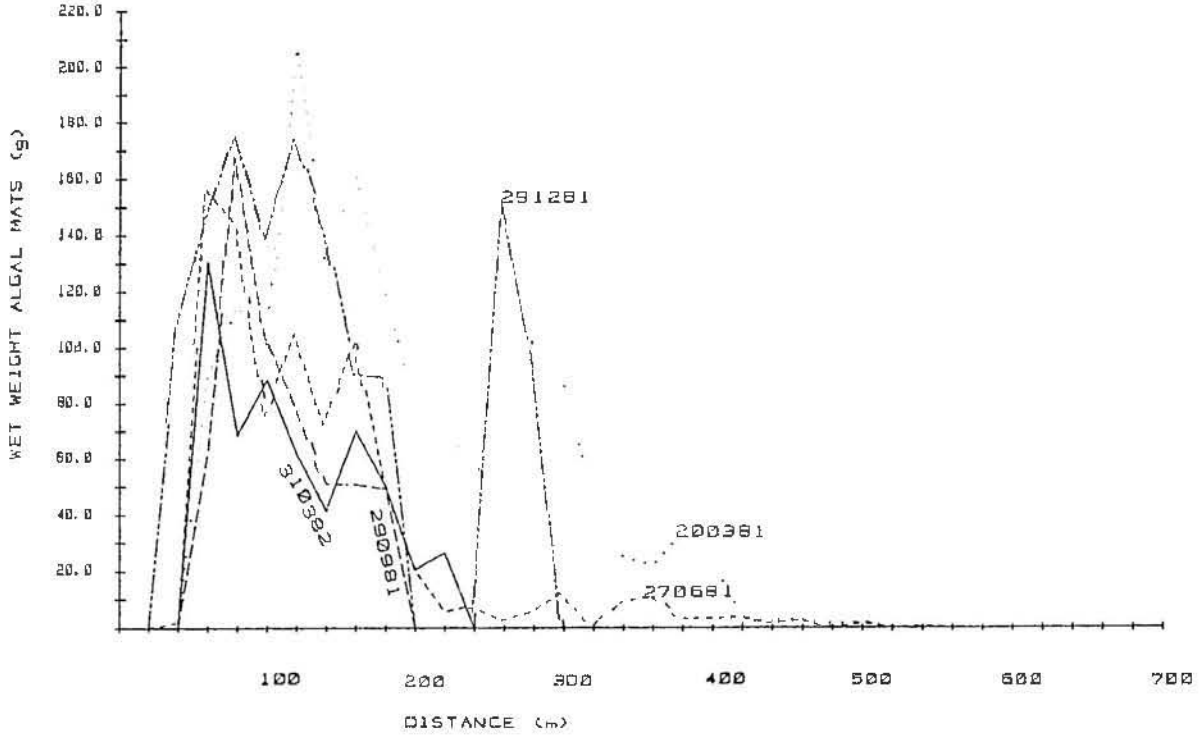


Fig. 2.6 Distribution of *Synechococcus / Oscillatoria* algal mats on transect sampling dates.

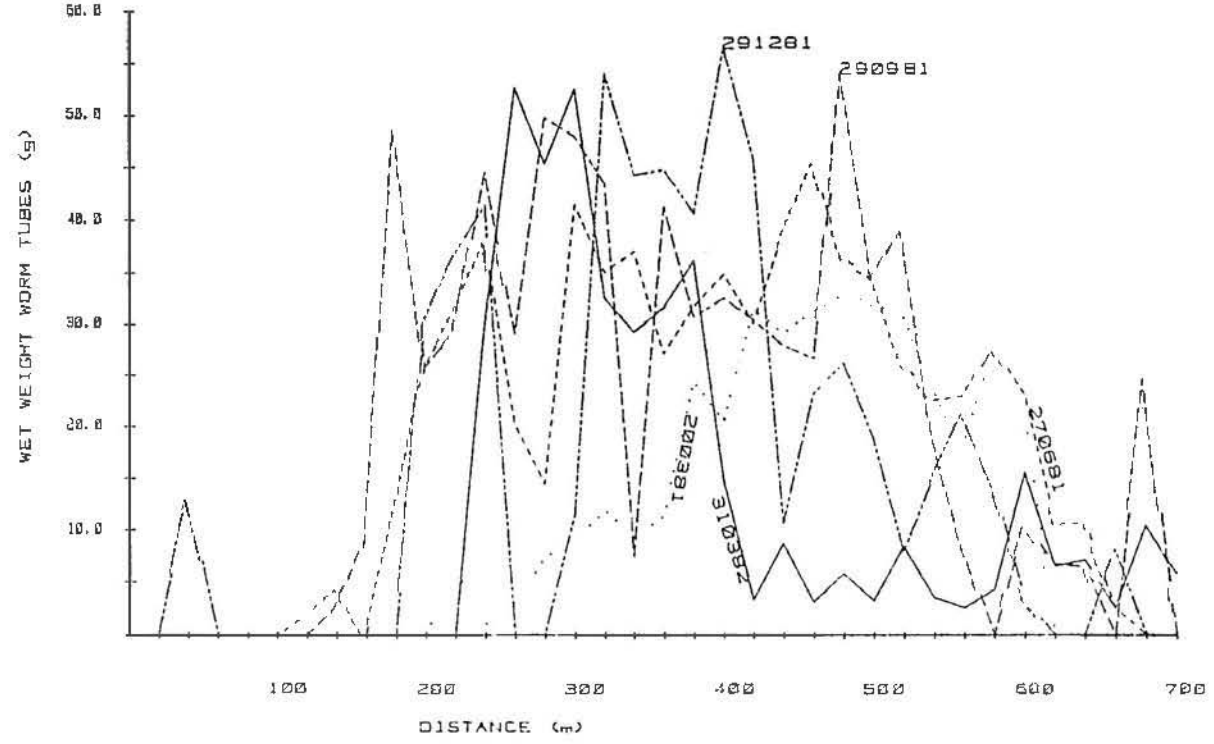


Fig. 2.7 Distribution of polychaete worm tubes on transect sampling dates.

single, broad peak centered on 500 m. On 270681 a sharp peak at 200 m is followed by a broad peak between 300 m and 450 m. There are two similar peaks on 290981, at 250 m and between 350 m and 450 m respectively, and on 291281, at 200 m and between 300 m and 400 m respectively. On 310382 there is a single, broad peak centred at 300 m. There are marked differences between the 200381 and 310382 distributions of worm tubes, indicating a lack of annual consistency.

2.3.1.7 Substrate surface temperatures

The minimum and maximum temperatures recorded at the 100 m interval sampling stations are shown in Fig. 2.8. The sampling dates fall approximately at the centre of the seasons they identify. Thus, 291281 lies close to the warmest, and 270681 close to the coolest, part of the year. Both 200381 and 310382 are midway between the decline in temperatures from the summer maximums to the winter minimums and 290981 is midway between the ascent from the winter minimums to the summer maximums.

In general, the minimum temperatures are considerably more variable than the maximum temperatures. The extremes of the temperature range appears to be largely determined by the horizontal distance down the beach, with a general decrease in the extremes from 0 m to 700 m. This is particularly marked by the minimum temperatures. Vertical position is less important than horizontal position and, for example, the 500 m station is less extreme than, say, 200 m even though it is vertically higher. It appears that the temperature range is not a simple function of aerial exposure.

2.3.2 Biota

A total of 15 species of molluscs were recorded during the sampling program as occurring more than 5 times; those species were defined to be the mollusc assemblage. A number of common non-molluscan species (e.g. amphipods, polychaete worms) have not been considered.

The defined mollusc assemblage consists of 4 bivalve species, 11 gastropod species and 1 species of anenome.

A list of the species belonging to the defined assemblage, together with their working abbreviations, follows:

1. *Notoacmea alta* Oliver, 1926 [Na]

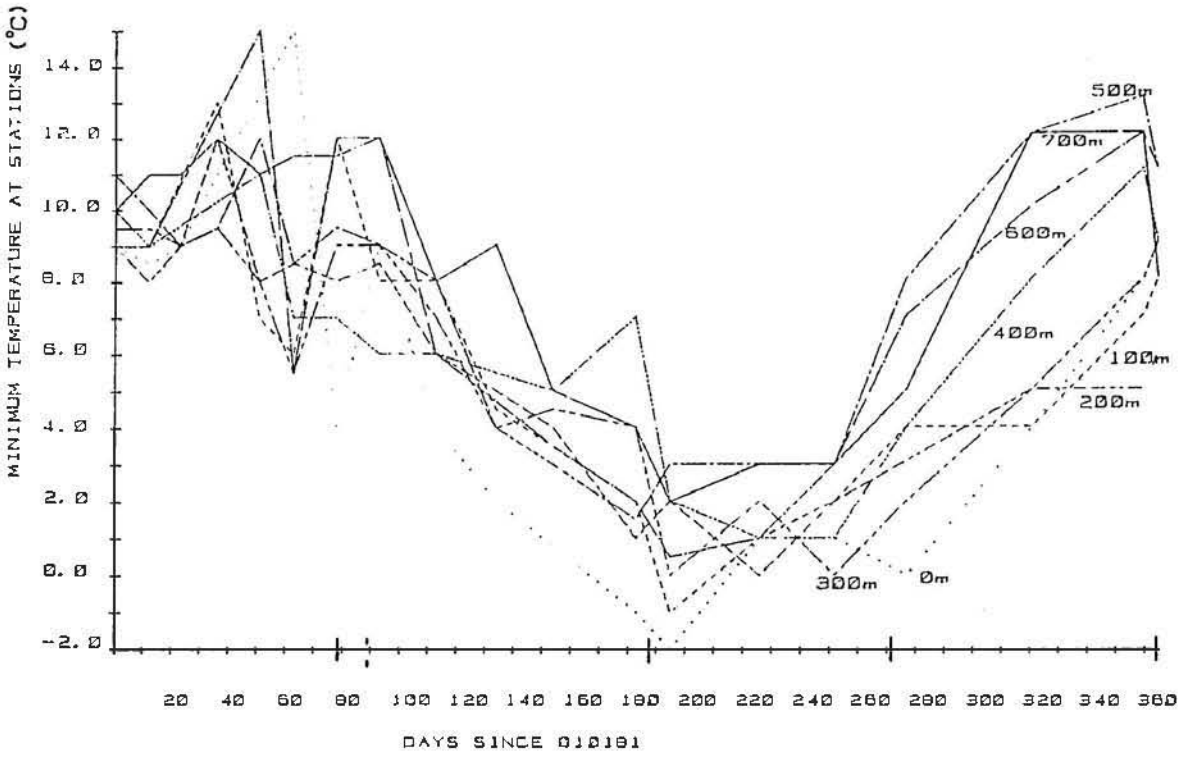
Class Gastropoda, Family Acmaeidae

2. *Austrocochlea constricta* (Lamarck, 1822) [Au]

Class Gastropoda, Family Trochidae

3. *Bembicium auratum* (Quoy and Gaimard, 1834) [Ba]

Class Gastropoda, Family Littorinidae



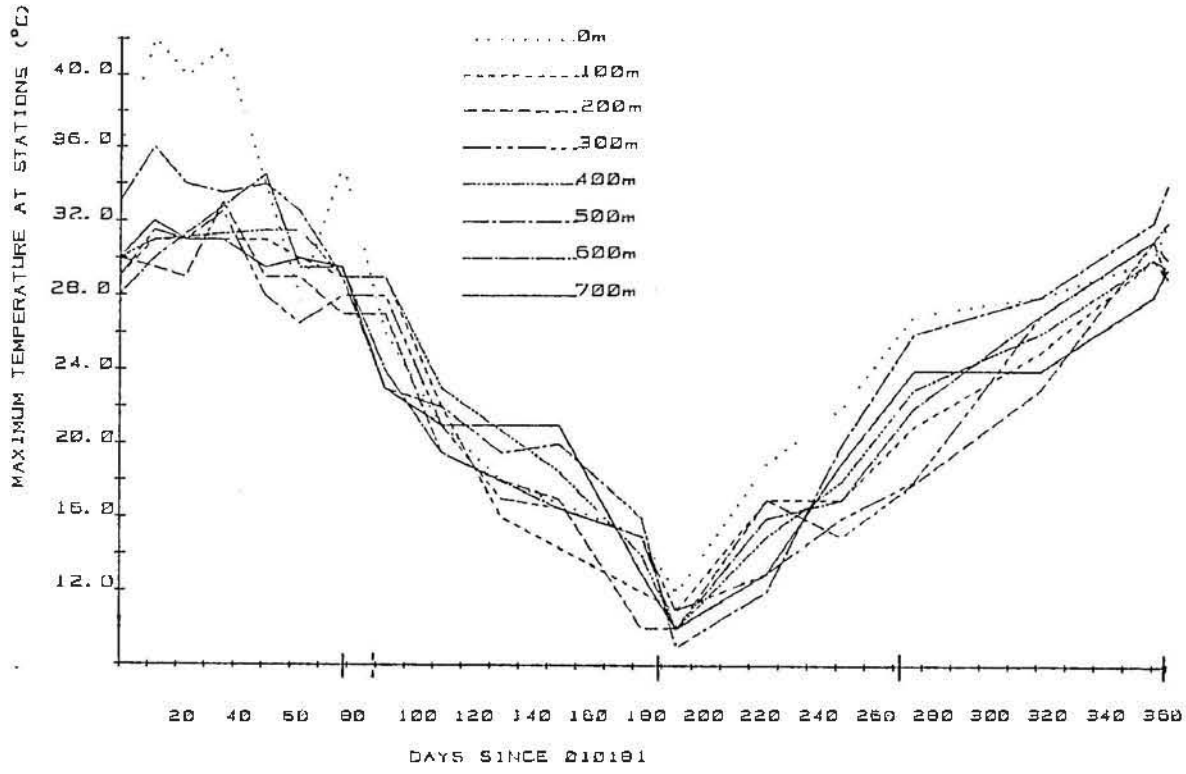


Fig. 2.8 Minimum and maximum substrate surface temperatures at the 100 m-interval stations during the transect sampling year. Sampling dates are marked on the time axis.

4. *Rissopsis consobrina* (Tate and May, 1900) [Rc]

Class Gastropoda, Family Rissoidae

5. *Microdiscula charopa* (Tate, 1899) [Mc]

Class Gastropoda, Family Skeneopsidae

6. *Hydrococcus brazieri* (Tenison-Woods, 1876) [Hb]

Class Gastropoda, Family Hydrococcidae

7. *Zeacumantus diemenensis* (Quoy and Gaimard, 1834) [Zd]

Class Gastropoda, Family Potamididae

8. *Agatha metcalfi* (Pritchard and Gatliff, 1900) [Am]

Class Gastropoda, Family Pyramidellidae

9. *Nassarius pauperatus* (Lamark, 1822) [Np]

Class Gastropoda, Family Nassariidae

10. *Cylichnina pygmaea* (A. Adams, 1854) [Cp]

Class Gastropoda, Family Retusidae

11. *Salinator fragilis* (Lamarck, 1822) [Sf]

Class Gastropoda, Family Amphibolidae

12. *Wallucina assimilis* (Angas, 1867) [Wa]

Class Pelecypoda, Family Lucinidae

13. *Katelysia scalarina* (Larmarck, 1818) [Ks]

Class Pelycypoda, Family Veneridae

14. *Anapella cycladea* (Larmarck, 1818) [Ac]

Class Pelecypoda, Family Donacillidae

15. *Solatellina biradiata* (Wood, 1815) [Sb]

Class Pelecypoda, Family Sanguinolariidae

16. *Anthopleura aureoradiata* [Aa]

Phylum Coelenterata, Class Zoantharia, Family Actiniidae.

The species abundance distribution of the assemblage, derived from pooled sampling data, is shown in Fig. 2.9. Fig. 2.10 depicts the overall zonation patterns from the pooled distribution transect data.

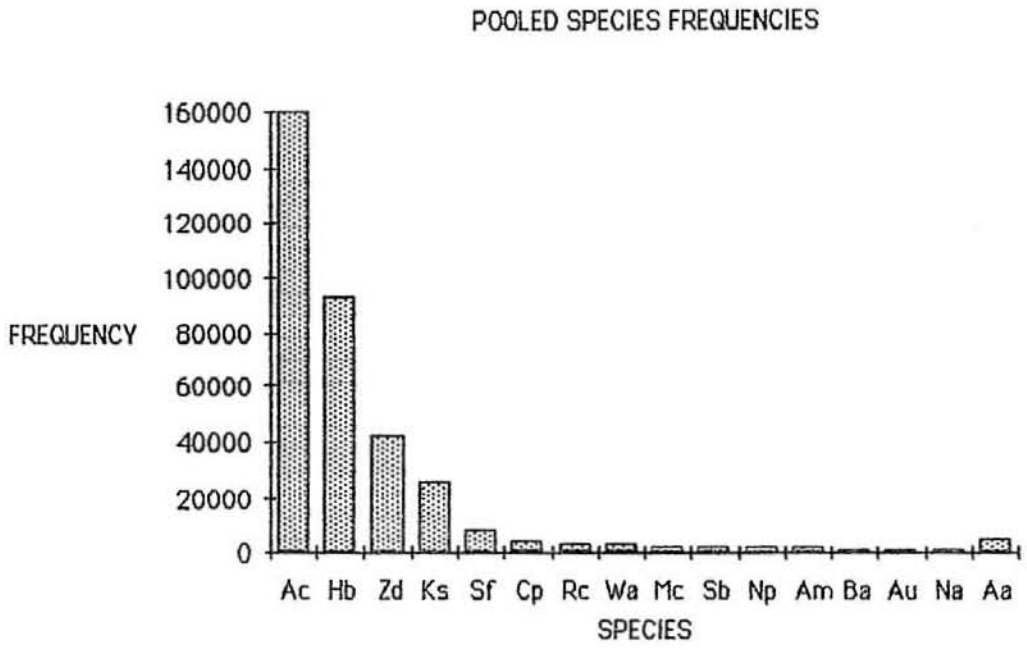


Fig. 2.9 Species abundance distribution derived from pooled distribution and dispersion transects. Molluscs are ranked from the most to the least abundant.

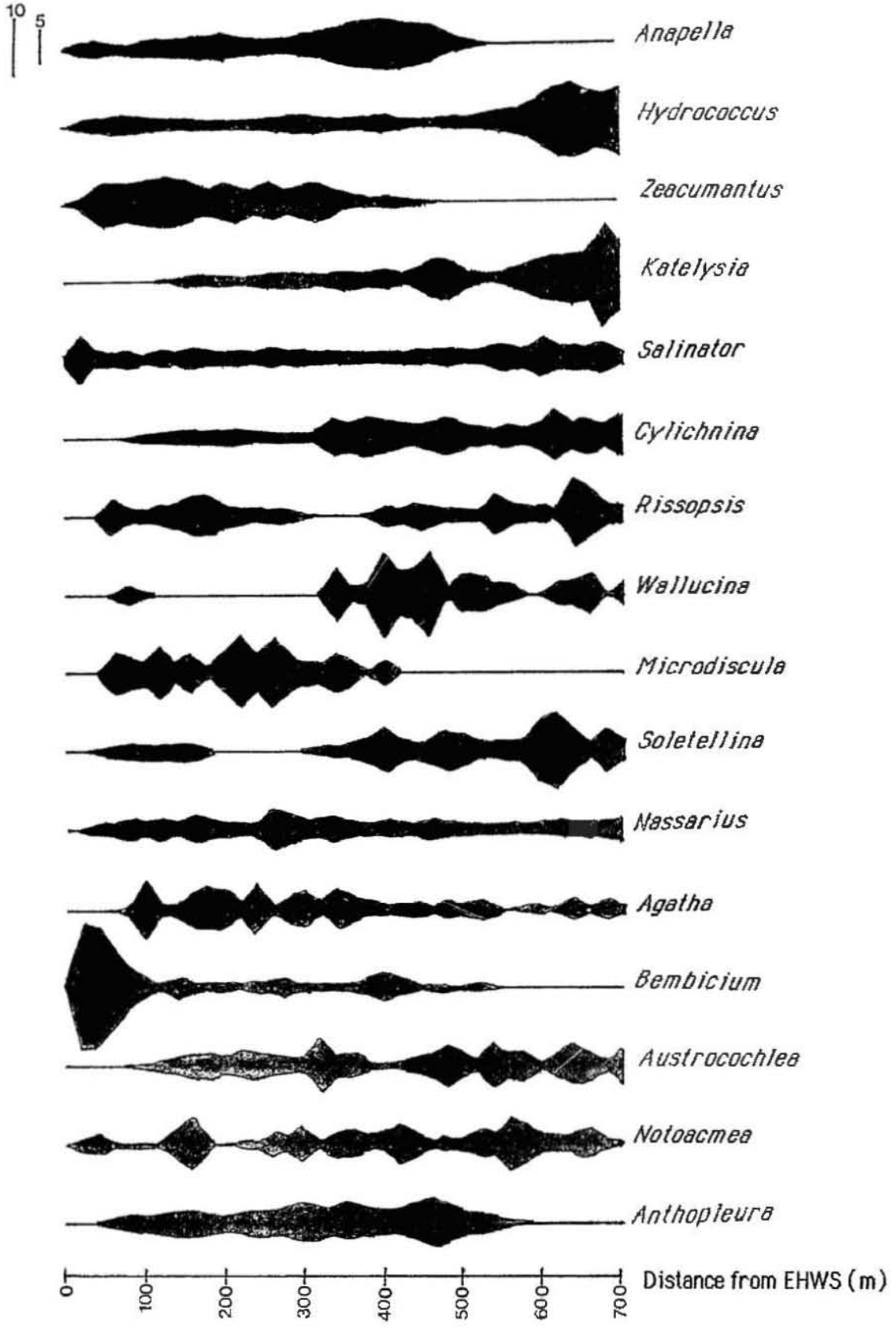


Fig. 2.10 Pooled species abundances along sampling transect. Molluscs are listed in order of overall abundance.

2.4 Discussion

2.4.1 Physical parameters

The intertidal beach of Pipe Clay Lagoon shows affinities with both the 'intermediate longshore bar-trough' and the 'intermediate ridge-runnel' states described by Short and Wright (1983). These states represent the highest and lowest energy intermediate states respectively (Short 1979). The beach states described by those workers are generally applicable to open sandy beaches and the enclosed nature of Pipe Clay Lagoon will negate their relevance to some degree; nevertheless they provide a useful reference standard.

During sampling, it was noticed that there was an accumulation of decomposing *Zostera* deep within the zone 5 beach ridge. Guiler (1950) recorded a healthy *Zostera* bed in that region some 35 years ago. It was not possible to determine for how long the *Zostera* had been decaying, but its proximity to the anoxic layer of the substratum suggests the time scale should be measured in years. Jørgensen (1977) determined that an organic pool of *Zostera* detritus would theoretically require 5 to 10 years for complete mineralisation, compared with 3 to 5 years if oxygen uptake is included. This, together with the negligible changes detected in the beach profile over a period of 15 months, suggests that the high beach ridge centred on the 500 m mark has existed for at least 10 years. The original *Zostera* bed is likely to have been responsible for the initial accumulation of sediments, which gradually built up in a self-perpetuating process.

Between the upper beach slope and the high beach ridge, lies an area of virtually horizontal substrate. This is also the zone of high densities of polychaete worm tubes. These are known to stabilise marine sediments and during sampling it was noted that they act to bind the substrate of Pipe Clay Lagoon.

It is likely, therefore, that the observed profile of the lagoon beach has existed in virtually the same form for a considerable number of years. Although it can be compared with standard beach types, such as those described by Short and Wright (1983), it is unlikely that wave and current action are solely responsible for its present form. The beach topography would be determined by dynamic processes and it is probable that the distribution of features such as *Zostera* beds and polychaete worm tubes are initially dependent on that topography but, once established, they act to dampen further changes.

The suggested constancy of the beach topography undoubtedly has important implications for the biota; these will be considered later.

An important difference between wave action on open and shallow (eg. lagoon) beaches is the asymmetrical nature of waves passing through shallow waters, and this can force material out of the bed into the overlying waters (Swart 1983). Other factors associated

with shallow sediments include their susceptibility to strong wind and tide induced currents. The expected result of these factors would be a continual sorting of the sediments. This appears to be the case at Pipe Clay Lagoon. At all distances and in all seasons, the sediments can be classed as 'well sorted', after Gray (1981). The constancy of the sorting coefficients along the transects indicates relatively constant sorting action with respect to both season and the position on the beach.

Areas of high energy wave action on a beach tend to have high median grain sizes (Swart 1983). Conversely, areas of low wave energy could be expected to accumulate fine particles. On the Pipe Clay Lagoon tidal flat, there are areas of finer sediments on the up-beach sides of the two beach ridges, particularly near the 250 m mark. These areas probably do represent relatively low energy regions, being protected on their seaward sides by the beach ridges. Greater wave energy in the lower half of the beach could account for the coarser sediments above the 500 m ridge, relative to those above the 300 m ridge.

The steepest regions of the beach, the upper and lower slopes (zones 1 and 6), are characterised by a comparative abundance of coarse sand particles. Flemming and Fricke (1983) noted that, at similar energy levels, coaser sand tends to form a steeper slope than finer sand, and this appears to be true at Pipe Clay Lagoon. The principal sediment fraction, which accounts for over 80 % of the sand particles shows a gradual increase in abundance down the transects while the smaller size fractions decline. This probably reflects the increasing wave energy experienced by the lower beach zones.

The distribution of shell debris also appears to reflect variations in wave energy. The irregular shape and low density of shell debris would make it particularly susceptible to displacement by water currents. A relative loss of energy experienced by waves passing up the beach slopes and over the beach ridges is probably responsible for the deposition of shell debris against those slopes and above those ridges. The greatest mass of shell debris is carried high onto the beach where wave energy would be finally expended.

Similar factors are likely to be responsible for the accumulation of algal mats against the upper beach slope. Although the mats bind with sedimentary particles to form an algal/sand matrix, they remain mobile and are able to be transported by water currents. In some beaches (Reise 1983) the feeding funnels of polychaetes can allow the anchorage of (green) algal mats in the sediment. The mutual exclusiveness of the algal mats and worm tubes, however, indicates that this does not occur in Pipe Clay Lagoon. In the 200381 autumn and also in summer, there is a secondary peak in algal mat abundance above the 300 m beach ridge, again possibly a result of current deposition.

During preliminary sampling, a 1 m^2 area of substrate was removed to the anoxic

layer (c. 5 cm). Within a few tidal periods, the algal mats had collected in the depression, eventually filling it to the level of the substrate, protecting the depression. The resultant square of algal mats remained patent for over 9 months. Deep in the accumulated mass of algae, a sulphide layer developed which would have greatly affected the microdistribution of any fauna. Similar accumulations occurred periodically in natural depressions. However, the small size of these depressions appeared to be insufficient to allow long term build up of algae and the depressions were generally obliterated during storms.

Although blue-green algal mats are common in intertidal areas, increased wetting of the mats leads to an increase in mat thickness, with an increasing dominance of filamentous forms (*Oscillatoria*) over non-filamentous forms (*Synechococcus*) (Potts 1980). The realised abundance of the algal mats on Pipe Clay Lagoon, then, probably represents a compromise between current-induced exposure and the more advantageous submergence. The seasonal differences in overall algal mass indicate a late summer bloom. Guiler (1950) noted similar seasonal variations in the lagoon.

The approximate parallels between the distribution of organic content in the sediments and the beach profile suggest that the organic carbon is comprised of particulate matter which is subjected to the same depositional forces as the sand particles. Weliky *et al* (1983) noted the difficulties in partitioning total marine sediment carbon between organic carbon and inorganic carbon; attempts to selectively remove one carbon fraction (eg. burning organic carbon at 500 ^{0}C) usually affect the remaining phase also. The possibility of the apparent organic content in the lagoon sediments, as determined by ignition loss, being influenced by the combustion of inorganic carbon cannot be dismissed. However, apart from high values of both parameters on the upper slope, the distributions of shell debris and percent ignition loss are dissimilar. By following the methods of Byers *et al* (1978), who suggested the lower ignition temperature of 475 ^{0}C, the unwanted burning of carbonate carbon appears to have been minimised.

Usually, the distribution of organic carbon is similar to the distribution of fine sedimentary particles (Pugh et al 1974; Tietjen 1977; Tsuchiya and Kurihara 1980). In Pipe Clay Lagoon, however, this does not appear to be the case. While the smallest particles show great variability in both time and space, with little trend, the organic content shows less variability in both dimensions and also exhibits consistent trends. The peaks identifiable in the organic content distributions do not correspond with peaks in the distributions of any sedimentary size fraction. Rather, they occur in similar positions to the peaks in the gross beach topography, suggesting the organic particulate matter is subjected to the same depositional forces as the bulk of the sediment. This is probably a

reflection of the high sorting of the sediments.

The correspondence between organic matter and sediment deposition suggests that living organisms have little affect on the organic content of the lagoon substratum. Organic content often correlates strongly with bacterial biomass (Bolter *et al* 1981) and can also be influenced by the activities of the meiofauna and the macrofauna. Deposit feeders, for example, can reduce the organic matter content of the substrate by feeding while the production of faecal pellets allows high bacterial growth (Rhoads 1974; Tsuchiya and Kurihara 1980). Conversley, the availability of organic matter in the substrate often determines the abundance of deposit feeders, primarily through the bacterial populations which are the main food of deposit feeders (Gerlach 1978). In Pipe Clay Lagoon it appears that the distribution of organic content is largely independent of the distribution of living organisms and can be regarded as a physical process. The reverse relationship, where organism distributions are determined by organic content, may occur, however, and this will be examined later.

The substrate temperature of intertidal areas will be affected by the interplay between the different responses of the solid sediments and the interstitial and overlying waters to the heating through solar radiation and cooling through evaporation. While the seawater would act as a moderating agent for temperature extremes, the periodic exposure of an intertidal beach will greatly increase the variability of substrate temperatures, relative to sublittoral sediments.

With high aerial temperatures, there will be a rapid evaporation of seawater following the tidal retreat with a resultant decrease in the cooling potential of evaporation. Thus, the sediment would become more dependent on solar radiation and aerial temperatures for heating. In contrast, relatively cool aerial temperatures would allow the retention of interstitial water which could continue to act as a temperature moderator. That moderating effect could be expected to lead to lower variability in cool conditions compared with temperature variability in warm conditions. This appears to occur on the lagoon beach, with minimum temperatures being considerably less variable than maximum temperatures.

It is somewhat unexpected, however, that the extremes of temperature range are primarily dependent on the horizontal distance down the beach rather than the height (and hence aerial exposure) of the beach. This could be due to a moderation of the air temperature as the prevailing winds pass down the transect.

The changes in temperature variations with respect to distance down the transect could be expected to be paralleled by changes in desiccation stress.

2.4.2 Biota

Despite differences in identifications, the present intertidal community of the lagoon appears to be similar to that described by Guiler (1950). This is true for both the relative abundances of the species and also for their zonation. Unfortunately Guiler did not conduct detailed sampling and it is not possible to compare absolute abundances or abundances distributions down the transect.

The observed community also shows considerable similarities with the molluscan communities on the tidal flats of Oyster Harbour and Princess Royal Harbour in the Albany area of Western Australia (Roberts and Wells 1980; Wells and Roberts 1980; Wells and Threlfall 1980). The similarities occur in species number, species composition and also relative abundances. The above habitats are very similar to that provided by Pipe Clay Lagoon, although Oyster Harbour has a permanent freshwater input (Roberts and Wells 1980).

South-eastern Tasmania lies in the distinct biogeographical Maugean Province (Edgar 1984) and Albany lies in the Flindersian Province (Knox 1963; Dartnall 1974) but the two provinces grade into each other (Knox 1963) and the Flindersian Province is considered to have cool temperate affinities, distinctly so in southern Tasmania (Bennett and Pope 1953). This is strongly supported by the present work.

The most abundant mollusc on Pipe Clay Lagoon, the bivalve *Anapella cycladea*, commonly occurs in sheltered areas of Tasmania, New South Wales and South Australia (Macpherson and Gabriel 1962) and is particularly common in Tasmanian east coast lagoons (Kershaw 1958; May 1958). Guiler (1950) did not detect *Anapella* as high on the shore as was observed in the present study, but his sampling methods were less intensive and he probably only included large individuals in his survey. *Anapella* is an obvious suspension feeder and lies buried with only its two short siphons extending to the surface.

Katelysia scalarina is also a suspension feeder (pers. obs.; Poore and Rainer 1974) and has a similar distribution to *Anapella* but it is also common in Victoria (Macpherson and Gabriel 1962). Guiler (1950) recorded *Katelysia* in Pipe Clay Lagoon under the name *Marcia* (Kershaw 1958) with a similar zonation to that found in the present study. Wells and Threlfall (1980) and Wells and Roberts (1980) noted similar zonations of *Katelysia scalarina* in Oyster and Princess Royal Harbours, with abundances steadily increasing down the beach.

The other bivalves on the Pipe Clay Lagoon tidal flat, *Wallucina assimilis* and *Soletellina biradiata*, are suspension feeders and surface deposit feeders respectively

(Poore and Rainer 1974). Little is known about their ecology in Tasmania.

Hydrococcus brazieri, the second most abundant mollusc and the dominant gastropod of the lagoon, is probably a deposit feeder (Wells and Threlfall 1982b). It is frequently buried in the top layer of the sediment and this could explain the apparently patchy distribution observed by Guiler (1950) (identified as *Assiminea*). The more intensive studies of Wells and Threlfall (1980) in Oyster Harbour reveal a wide distribution over the tidal range, although the greatest abundance occurs near the middle of the beach, in contrast to the distribution observed in the present study. *Hydrococcus* (*Assiminea*) is common in the sheltered waters of Tasmania (Kershaw 1958).

The distribution of *Zeacumantus diemenensis* in Pipe Clay Lagoon differs significantly from that in Princess Royal Harbour. In the latter habitat it reaches its greatest abundance in the lower areas of the beach (Wells and Roberts 1980). Guiler (1950) appears to have identified this species as *Bittium* in Pipe Clay Lagoon, which showed similar zonation to the present-day animals. *Zeacumantus* feeds in a similar manner to *Hydrococcus*, pushing through the substrate, but it probably consumes algae and Foraminifera rather than bacteria and detritus. Related species are known to have algal diets (Graham 1955; Steneck and Watling 1982) while J.L. Hickman (pers. comm.) has frequently observed masses of Foraminifera in the gut of *Zeacumantus*.

Salinator fragilis is common in the mid to upper littoral zone in sheltered marine inlets around the south-eastern Australian coasts (Smith and Kershaw 1979). It is also common in Princess Royal Harbour where it reaches its greatest abundance in the middle of the beach (Wells and Roberts 1980) while at Oyster Harbour it is distributed over much of the beach (Wells and Threlfall 1980). Guiler (1950) made similar observations to those of the present study, noting that *Salinator* reaches its greatest densities at the top of the Pipe Clay Lagoon tidal flat. Animals are also found in the supralittoral *Salicornia* herbland. *Salinator*, like many marine pulmonates (Graham 1955; Morton and Miller 1968), appears to feed mainly on detritus and pushes through the top layer of substrate; diatoms may also be consumed. Morton (1979) considered the Ellobiidae and other marine pulmonates to be unselective deposit feeeders.

Cylichnina pygmaea, an elongate 'canoe' shell, is a member of the actively rapacious group of bubble shells. Related species are known to prey on small bivalves (Macpherson and Gabriel 1962; Rudman 1970) while in the United Kingdom the pearl bubble, *Retusa obtusa*, feeds primarily on juvenile *Hydrobia ulvae* in habitats similar to that of Pipe Clay Lagoon (Smith 1967). The close affinity between *Retusa* and *Cylichnina* and *Hydrobia* and *Hydrococcus* suggest that similar trophic relationships

might occur in Tasmania. The small size of *Cylichnina* has precluded that species from previous ecological studies in Tasmania, including that of Guiler (1950).

Rissopsis consobrina is also a small animal and has not previously been found in Pipe Clay Lagoon but it is known to occur in the adjacent Frederick Henry Bay (May 1958). Rissoids feed on diatoms, microalgae, detritus and algal fragments (Graham 1955; Fretter and Graham 1962; Steneck and Watling 1982). In Pipe Clay Lagoon *Rissopsis* is notable for its green colouration, visible through a semi-transparent shell. This suggests that algae form the principal diet, probably microalgae although the *Synechococcus / Oscillatoria* mats cannot be discounted as a potential food source.

Microdiscula is a minute animal, with a maximum size of approximately 500 µm. It is therefore not surprising that virtually nothing is known about its ecology apart from May (1958) noted that it is common below depths of 20 m (even in the present study, numerous animals undoubtedly passed through the 500 µm sampling mesh). A related northern hemisphere species, *Skeneopsis planorbis*, feeds on filamentous algae or rasps off diatoms attached to such algae (Ankel 1936, cited by Graham 1955; Steneck and Watling 1982); algal cells and diatoms may also be rasped off rocks (Fretter 1948).

The widely distributed *Nassarius pauparatus*, like other dog whelks, is carnivorous and feeds mainly on carrion (pers. obs.; Guiler 1950; Graham 1955; Poore and Rainer 1974). In the present study, *Nassarius* was frequently observed to also feed on living *Anapella*, apparently drilling between the valves. Macpherson and Gabriel (1962) noted that related species can readily bore through the actual shells of molluscs to feed. This probably occurs in Pipe Clay Lagoon since a large proportion of empty bivalve shell possessed drill holes. The only other known candidate for shell drilling in the lagoon is *Polinices conicus,* but only one specimen was found in the intertidal area.

There appears to be little zonation of *Nassarius* populations in the lagoon; this was also noted by Guiler (1950). *Nassarius* is common in Oyster Harbour but apparently shows no vertical distribution trends, the major factor controlling its distribution appearing to be salinity rather than exposure (Wells and Threlfall 1980).

The Pyramidellidae, including *Agatha metcalfi*, have mouthparts modified for piercing and sucking (Fretter and Graham 1949 a,b; Morton 1979) and Fretter and Graham (1949 b) considered it likely that there is little variation in feeding methods throughout the family. Each Pyramidellidae species appears to be a host-specific ectoparasite, peircing the host's tissues with a stylet and sucking the tissue fluids up by means of a buccal pump. Hosts may include bivalves, tube polychaetes and coelenterates (Pelseneer 1914, cited by Fretter and Graham 1949 a; Lebour 1932).

Agatha was not found in Guiler's (1950) survey but May (1958) suggested it is probably well distributed in the shallow waters of Tasmania. Related species occur in Port Phillip Bay, Victoria (Poore and Rainer 1974) and also in Oyster Harbour and King George Sound, near Albany (Roberts and Wells 1980).

Bembicium auratum is found chiefly in high in the tidal range in estuaries, sheltered bays and inlets and is a member of a complex of species that includes *B. nanum* and *B. melanostoma* ; these species separate according to the habitat with *B. nanum* occuring on rocky shores and *B. melanostoma* on stenohaline mudflats (Anderson 1958). *B. auratum* is the most adaptable to salinity changes and can also suvive for 3 months out of water (ibid). An absence of desiccation tolerance in juvenile forms is overcome by a retention of the primitive habit of spawning in pools (Anderson 1962). *Bembicium* has a wide distribution in southern Australia (Macpherson and Gabriel 1962) and was recorded in Oyster Harbour, Princess Royal Harbour and King George Sound (Roberts and Wells 1980).

Guiler (1950) appears to have identified *B. auratum* as *B. melanostoma* in Pipe Clay Lagoon and noted a distribution pattern similar to that observed in the present study. Although the pooled abundances of *Bembicium* are relatively low, this is not a true indication of its dominance at the top of the lagoon beach. In the first 40 to 50 m, *Bembicium* is the most abundant mollusc in a zone where only *Salinator* is also abundant.

Anderson (1958) found dead and decaying vegetation, unicellular plants and animals, algal spores and bacteria in the gut of *Bembicium*. It is likely, however, that the main food source is microalgae (Branch and Branch 1980) as it is in many littorinids (Steneck and Watling 1982).

Austrocochlea constricta was found by Guiler (1950) to occur over most of the lagoon beach, with numbers slightly higher near the bottom of the transect. Similar findings were made in the present study. The main controlling factor on its distribution in the lagoon, however, appears to be the availability of solid substrate; numbers were greatly increased on rocky outcrops, some distance from the transect. *Austrocochlea* is common throughout southern Australia (Macpherson and Gabriel 1962). It achieves high abundances in Oyster Harbour where it shows zonation patterns similar to those in Pipe Clay Lagoon (Wells and Threlfall 1980). Underwood (1975) also found similar zonation patterns on sheltered shores in New South Wales but observed that shore height is not a distribution determinant on exposed shores.

The predominant diet of *Austrocochlea* is diatoms (Creese and Underwood 1976)

although microalgae are also likely to be a food component, as they are in numerous other trochids (Steneck and Watling 1982).

Limpets are generally associated with hard substrata. Indeed, only epizoic habits allows *Notoacmea alta* to survive on the lagoon tidal flat. Guiler (1950) appears to have identified this species as *Patelloida subundulata* and noted similar habits. Such habits have also been observed in Victoria and South Australia (Macpherson and Gabriel 1962). In the lagoon the preferred substrate of *Notoacmea* appears to be *Austrocochlea* and their similar distributions are probably a reflection of this. *Notoacmea* presumably grazes the algal growth that forms on the shell of *Austrocochlea* .

Little is known about the ecology of the anenome, *Anthopleura aureoradiata* . In New Zealand *Anthopleura* burrows in harbour flats and lives attached to bivalves or small stones (Morton and Miller 1968). In Pipe Clay Lagoon it attaches to *Anapella* , *Katelysia* and, to a lesser extent, *Austrocochlea* . Its distribution over the transect is probably related to the availability of hosts. During sampling it was noted that *Anthopleura* was less easily removed from *Anapella* , probably because the striations on *Katelysia* reduces the contact surface; *Anapella* is the preferred host. Anenomes are known to feed on small bivalves and gastropods (Minchin 1983) and these animals can all be found in the enteral cavity of *Anthopleura* . When feeding, *Anthopleura* lies level with the substrate and appears to trap wandering *Hydrococcus* and *Zeacumantus* juveniles. Juvenile bivalves could be swept onto the oral disk by water currents.

The pooled frequency distribution (Fig. 2.9) of the defined (molluscs and anenomes) community approximates a truncated log-normal distribution. This type of distribution is expected in communities where the relative importances of the species are determined by a variety of factors, each acting in partial independence (Whittaker 1972). Obviously the pooling of data through time and space inhibits strict interpretation of the importance value curve, but this is inevitable when trying to define a community that exists along an environmental gradient(s). In later chapters, intra- and interspecific interactions will be examined as they are expressed in the distribution and dispersion patterns of the species. These will be considered in the light of correlations between species distributions and changes in the physical parameters measured over the tidal flat.

CHAPTER 3

SEASONAL AND SPATIAL VARIATIONS IN POPULATION STRUCTURES

3.1 Introduction

This chapter examines the changes in the demographic struture of each species, with respect to the time of year and the position on the beach. The reproductive biology of the Tasmanian populations of the study species has not been examined previously, but the demographic changes detected in this work allow recruitment patterns to be proposed. Variations in recruitment rates through time and space should be closely related to the distribution and dispersion patterns shown by each species, and hence to the structure of the assemblage.

Both the spawning and settlement of molluscan larvae are often dependent on environmental cues. In temperate seas spawning usually occurs over a large portion of the year, although considerable variation can be found between species in the same environment (Giese 1959). Small scale differences between members of the same species also occur, in relation to differences between microhabitats.

The spawning of bivalves, for example, may commence slightly earlier in high intertidal areas than in low areas (Seed 1969) while physical differences in the substrate, along an intertidal beach profile, may cause preferential settling of larvae (Quayle 1952). The actual reproductive effort of breeding adults may similarly be affected by the microhabitat. Some bivalves, for example, show an increase in reproductive activity in lower intertidal areas, possibly as a direct result of the increased availability of feeding time (Seed 1969). The same trophic factors may also account for different growth rates of animals in high and low tidal areas. This appears to be most marked in cool habitats, such as those of the Arctic (Green 1973). Although gastropods are typically more independent of the environment than bivalves are, gastropod recruitment is also influenced by habitat conditions. Gastropods, for example, may show variations in reproductive strategies according to the degree of exposure (Anderson 1962; Faller-Fritsch 1977).

The reproductive patterns of intertidal organisms, then, reflect both the

environmental and, to a lesser extent, structural features of the habitat and the constraints those parameters place on the reproductive potential of a given species.

While this study is not directly concerned with the reproductive biology of the species, the information provided by the distribution and dispersion transects allows an examination of seasonal changes in the demography of the populations at different shore levels in Pipe Clay Lagoon. The examination suggests general patterns of recruitment and growth, and the indicates the constraints imposed on those patterns by the degree of tidal exposure.

3.2 Methods

3.2.1 Introduction

Demographic studies of molluscs are usually based on a combination of three principal methods of age determination Haskin (1954).

The most direct method involves marking individual animals and following their growth over a period of time. This was not attempted.

An indirect method depends on the presence of well defined seasonal (e.g. winter) growth rings. Such rings usually mark seasons of increased allocation of energy to gametogenesis and are often pronounced in high latitude species. There may be additional rings caused by disturbance to the animal; added confusion can arise when winter rings become indistinct due to protracted sedimentary abrasion (Hughes 1970).

Many individual bivalves (particularly *Katelysia*) in Pipe Clay Lagoon show growth rings but no consistent relationship between shell size and the number of rings was found, other than the fact that larger animals tended to have more rings. In all species a considerable proportion of individuals lacked rings and this may be a reflection of the relatively mild winter conditions in comparison to waters of higher latitudes. The lack of consistency in the occurence of growth rings precluded their use for ageing individuals.

A second indirect method is based on temporal changes in the size frequency distribution of population samples. In populations with well defined seasons of recruitment and growth, distinct cohorts are often discernable in the size frequency distributions. These may be followed through time to allow estimation of the age, growth and mortality rates of the cohorts (e.g. Hughes 1970).

The analysis of size frequency distributions has received considerable attention and all common methods assume the distributions to be composed of one or more normal frequency distributions, each representing a cohort. Graphical methods vary from a simple inspection of modes (Tesch 1968) or plotting the cumulative frequencies on probability paper (Harding 1949; Cassie 1954), to more rigorous graphical methods (Macdonald and Pitcher 1979).

Hasselblad (1966) developed a computer algorithm using the principle of maximum likelihood to fit overlapping normal curves to a size frequency distribution (see also Macdonald and Pitcher 1979). The method is statistically superior to graphical procedures, particularly because it removes a great deal of the subjectivity from the analysis.

3.2.2 Initial analysis

Size frequency distributions of each species were constructed for each dispersion transect station (100 m to 700 m; 200381 to 291281) by pooling the abundances in all cells of the relevant grid.

Hasselblad's (1966) technique was applied to the size frequency distributions of those Pipe Clay Lagoon populations that showed evidence of a mixture of distributions.

Anapella and *Katelysia* always exhibited a numerical dominance of 0 mm animals, making the frequency distribution of the first cohort of each species approximate a left-truncated normal distribution. The complete distributions were therefore reflected about zero before analysis. The first cohorts could then be approximated by normal distributions centred on the 0 mm class with the negative component being ignored after the approximation. In no species, however, could the complete size frequency distribution be adequately represented by a mixture of normal distributions: Chi-square comparisons between the observed and expected frequency distributions were highly significant in all cases.

It was not possible to transform the size frequency distributions to normality because the frequency data was discrete, with too few size classes to allow for reclassification. Since transformation would only have the effect of altering the abscissa (size class) scale, no movement of frequencies from one class to another, as was required for transformation to normality, was possible without reclassification.

3.2.3 Final analysis

The size frequency distributions were therefore separated into groups by visual inspection. This was, of course, subjective, but in most cases the groups showed obvious cut-off points. Each group was approximated by a normal curve and the fit tested using the Chi-square test.

The first group of *Anapella* and *Katelysia* could not be fitted in this manner, even with reflection about the 0 mm size class, because the frequency peaks showed too much kurtosis. Kurtosis provides a measure of the departure from normality of a distribution and can loosely be regarded as a measure of the steepness of the reflected size frequency distribution. Strong leptokurtosis (high positive kurtosis) indicates a high proportion of small (and large) animals and a low proportion of medium size animals. Kurtosis is not directly related to the relative proportion of small (0 mm) animals since it is a measure involving the entire group. For *Anapella* and *Katelysia*, kurtosis of the reflected first group was taken as a measure of the relative dominance of 0 mm animals with respect to the whole group.

For those size class groupings that could be adequately represented by a normal curve, the mean, standard deviation, kurtosis and skewness of the group were calculated, together with the 95% confidence limits about the mean. In some cases the fit was poor but the Chi-square value sufficiently low (although significant) to warrant the inclusion of confidence limits. As Zar (1974) notes, the t-test, on which confidence limits are based, is sufficiently robust to handle minor violations of normality.

Skewness is a measure of the relative positions of the mean and mode of a distribution. If the highest frequency size classes are found above the mean, the distribution is negatively skewed, while a mode occurring below the mean indicates positive skewness. The skewness of a distribution (like the kurtosis) can be tested for significance (Snedecor and Cochran 1967) but, in the present analysis, skewness was treated only as an indicator of deviation from normality. Skewness and kurtosis were calculated for groups having at least 3 individuals but obviously good reliability of the indicator would require larger sample sizes. For the purposes of this study, any group of 3 or more individuals that showed strong positive skewness was regarded as having undergone an influx of young animals, while strong negative skewness was taken to indicate a prior period of growth, with relatively negligible influx. Since skewness and kurtosis were only considered as indicators of deviations of the size frequency distributions from normality, the calculated indices are not presented here.

The mean sizes of the (unreflected) size frequency distributions of the first group of *Anapella* and *Katelysia* were also calculated. In those groups, the mean size gave an indication of the overall age but because the frequency distributions were far from normal, t-test comparisons in the form of confidence limits were not applicable.

3.3 Results

3.3.1 *Anapella*

The size frequency distribution (Fig. 3.1) was separated visually into 2 groups:

Group 1 (0 - 6 mm)

The mean size of group 1 (Fig. 3.2) is relatively constant (0.6 - 0.7 mm) between 100 m and 400 m, except at 200381 when there is a steady decrease from c. 0.95 mm at 100 m to c. 0.60 mm at 400 m. Below 400 m the mean size is highly variable although the small number found at these stations makes those means unreliable. In general, however, there is an increase in mean size between 400 m and 600 m, prior to a sharp decrease at 700 m.

For group 1, then, the beach can be divided into 2 zones: 100 - 400 m and 400 - 700 m. The upper zone is characterised by an abundance of animals, with a general increase in dominance of 0 mm animals from 100 m to 400 m.

The smallest (0 mm) size class is represented at all distances throughout the year, suggesting continuous reproduction. The relative changes in abundance of 0 mm animals with respect to season varies from station to station.

There appears to be a wave of settling of 0 mm animals following 200381, passing from 400 m to 100 m and 400 m to 700 m with time before settling at all distances falls off in 291281 (the logarithmic transformation of the frequencies makes this less obvious). At 400 m the 0 mm class is always more abundant than at other distances; abundances are also more constant there.

At 400 m, there is little seasonal change in the kurtosis of the (reflected) size frequency distribution. Above and below 400 m the kurtosis is variable, particularly at 100 m and 300 m. Generally the cooler seasons are associated with higher kurtosis. This is a reflection of the changes in abundance of the 0 mm size class. The constancy of the 400 m kurtosis suggests that 400 m may be a 'refuge' or 'reservoir' for *Anapella* reproduction.

Group 2 (7 - 23+ mm)

At all stations where group 2 animals are common (100 - 400 m), there is a general decline in numbers from 200381 to 291281 (Fig. 3.1). For each season there is a general decline in abundance from 100 m to 400 m, although in each case there is an increase from 200 m to 300 m before a sharp fall to 400 m. Numbers are constant at 300 m and 400 m while at 100 m and 200 m numbers decrease from 200381 to 291281. Thus, at 100 m and 200 m, the changes in abundance of group 2 animals from 200381 to 291281 (-ve) are opposite to the changes in 0 mm animals (+ve).

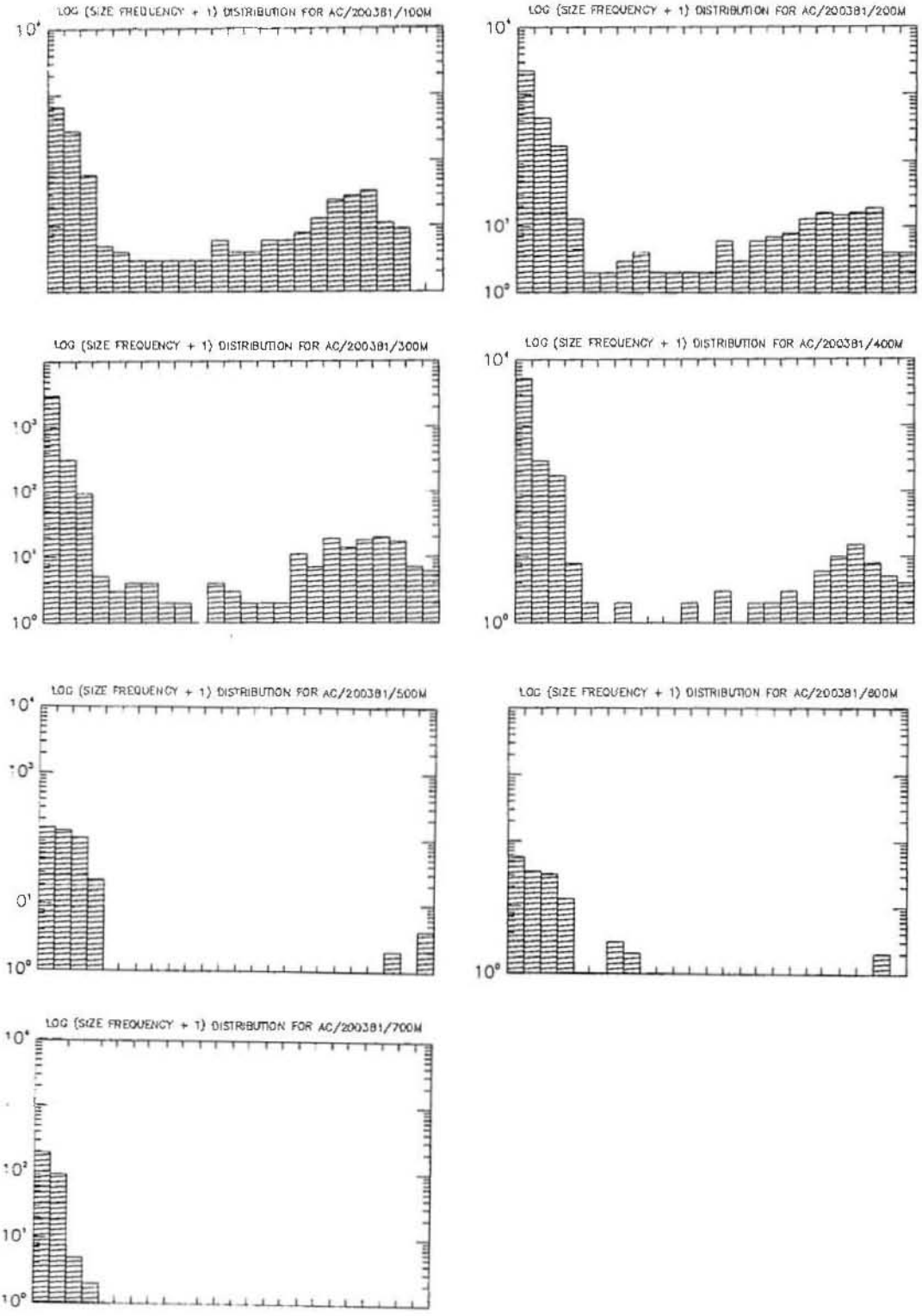


Fig. 3.1 Size frequency distributions of *Anapella* at dispersion transect stations. Size class axes range from 0 mm to 23+ mm in 1 mm intervals.

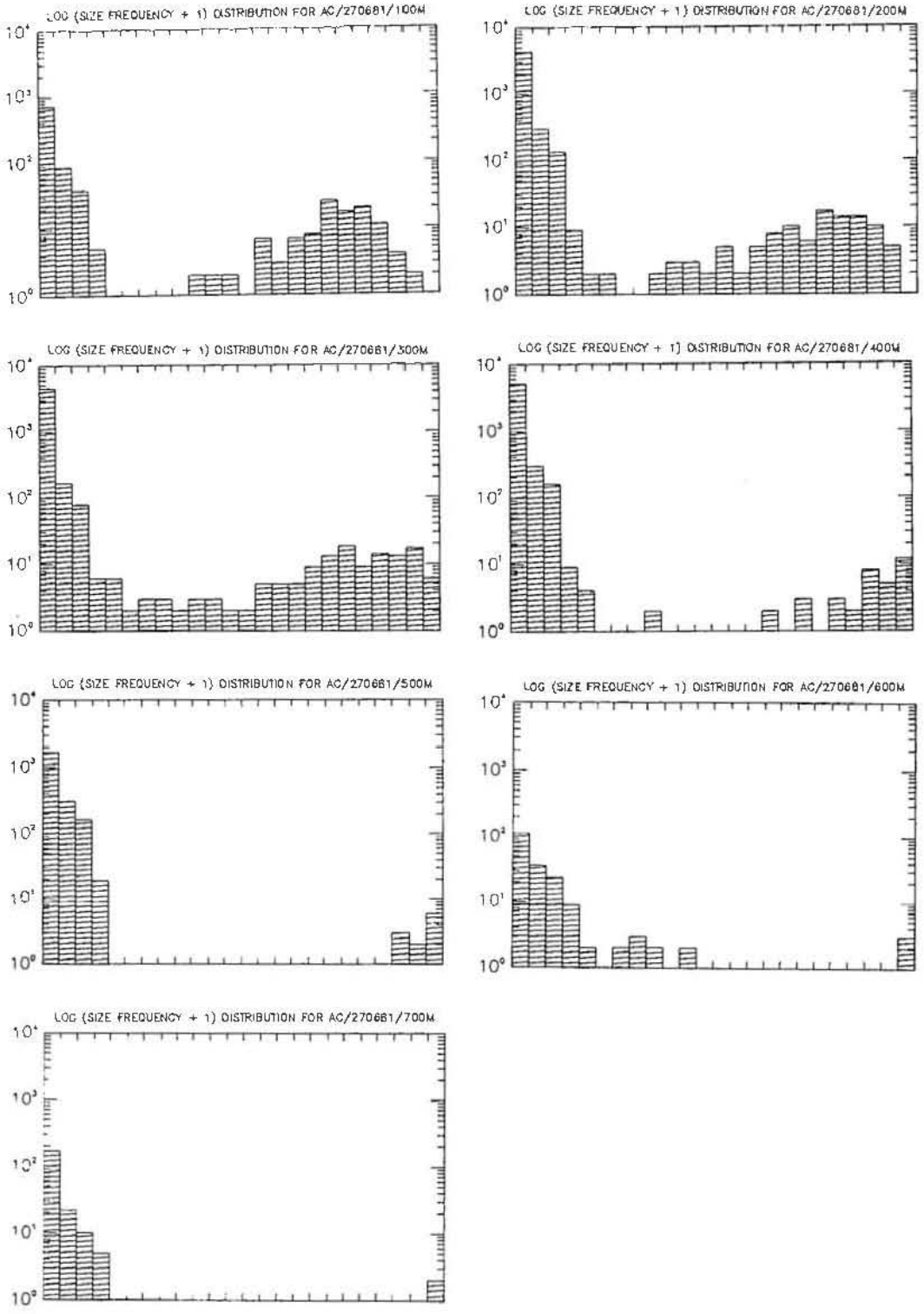


Fig.3.1 (continued)

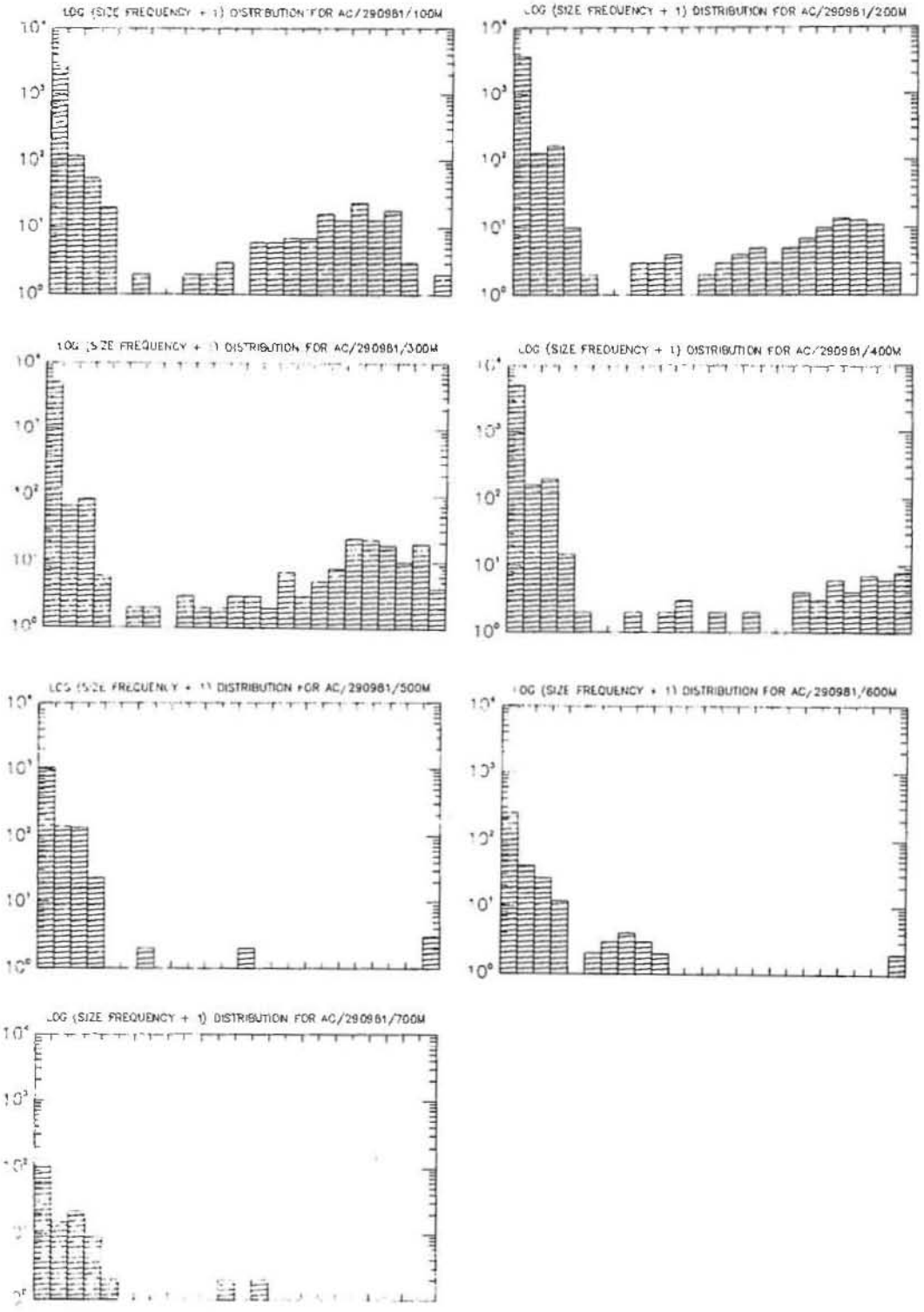


Fig. 3.1 (continued)

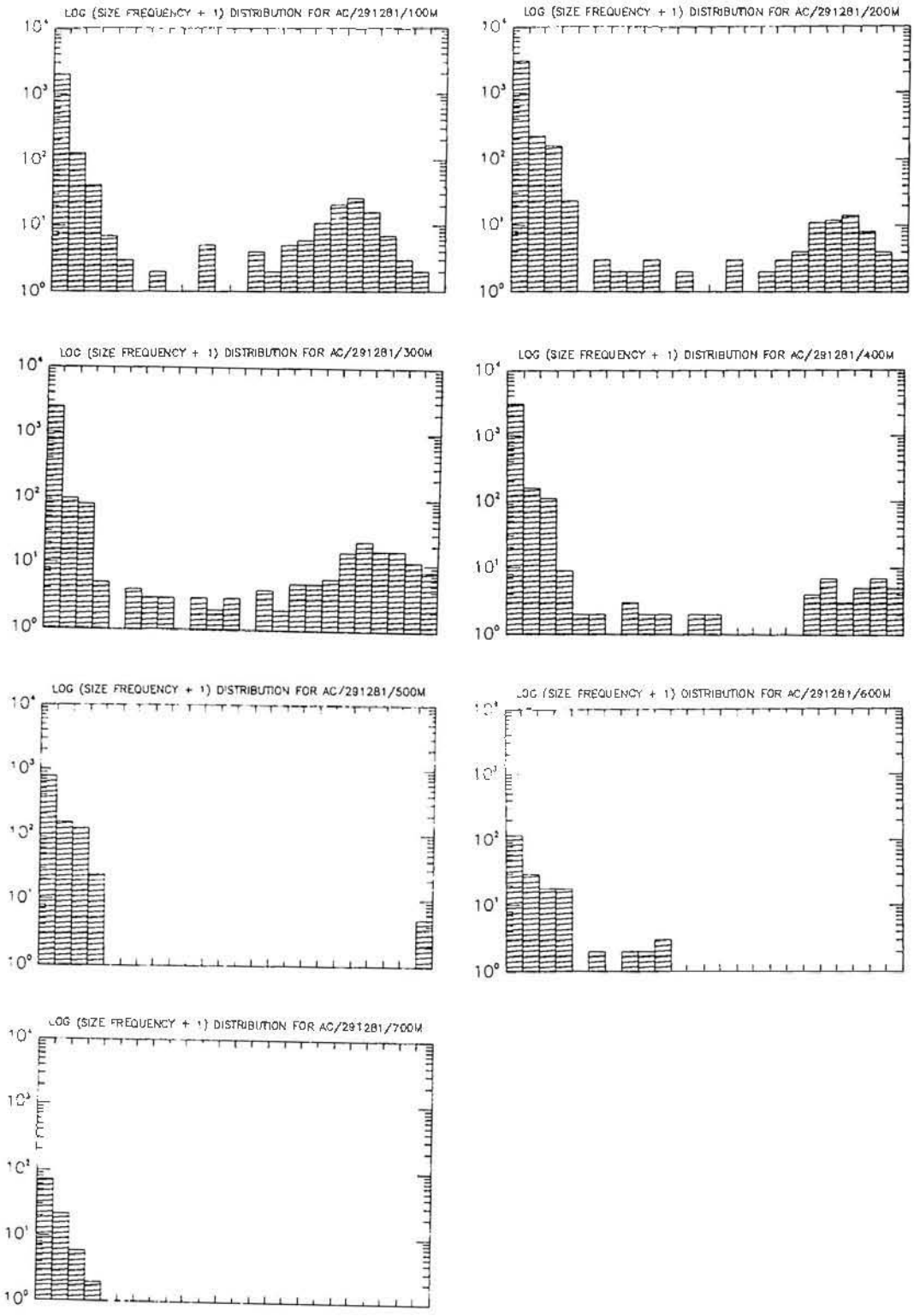


Fig. 3.1 (continued)

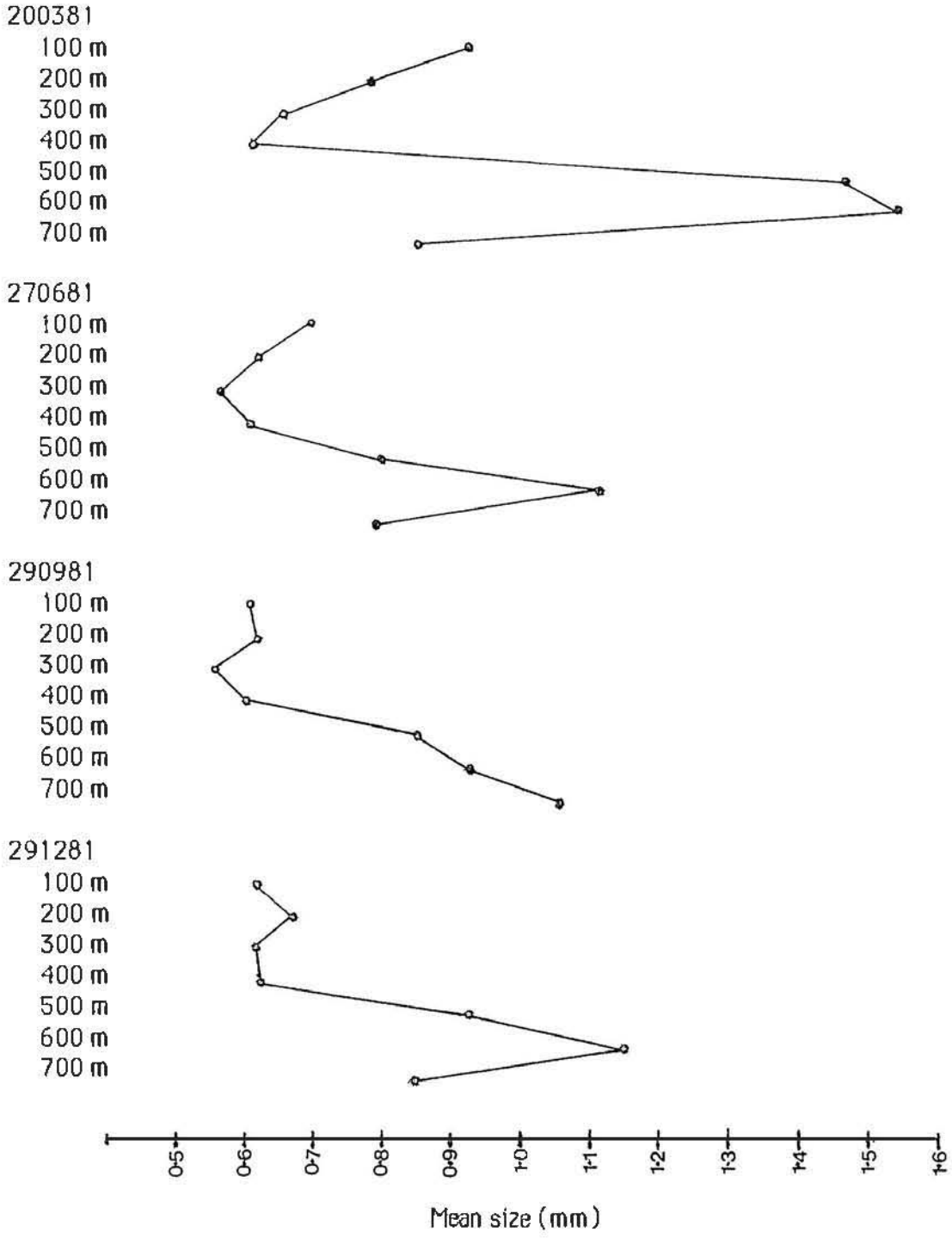


Fig. 3.2 Changes in the mean size of *Anapella* group 1 animals over the transect and through the seasons. No confidence limits given due to the non-normality of this group.

For each season there is a general decrease in the mean size of group 2 animals (Fig. 3.3) from 100 m to -400 m, although at a given distance the mean size changes little throughout the year.

There is a general decrease in negative skewness at 100 m from 200381 to 290981 followed by an increase to 291281. This is despite the decrease in the numbers of young group 2 animals (which would increase the negative skewness) over the same period. Alternatively, the negative skewness could be expected to increase from 290981 to an extrapolated 200382, despite a projected influx of young group 2 animals. This suggests that the summer months are a time of rapid growth of group 2 animals at 100 m following reduced growth rates over winter. In contrast, lower shore areas appear to have fairly steady growth rates over the year, as evidenced by a general increase in negative skewness throughout the year.

Summary.

The -400 m region of the beach appears to be a refuge area for *Anapella*. Although the numbers of adults (group 2) are low at 400 m, there is also a constant and high settling success of 0 mm animals.

The smallest size class (0 mm) is represented at all distances throughout the year but numbers increase with a wave of settling moving up from 400 m over the cooler part of the year. There is subsequently an increase in group 2 animals the following summer. These grow most rapidly high on the shore, although the mean size is smaller in high beach areas than in low areas. Following the summer influx of group 2 animals, there is a decrease in their number over the winter months. The decrease is most marked on the high shore.

In most respects the demographic patterns above 400 m are repeated below 400 m, at least until 600 m. The beach ridge at 500 m, followed by the sharp 600 - 700 m decline, complicates the pattern. The relative scarcity of group 2 animals below 400m, however, is significant.

3.3.2 *Katelysia*

The size frequency distribution (Fig. 3.4) was separated visually into 3 groups:

Group 1 (0 - 6 mm)

The mean size of group 1 *Katelysia* (Fig. 3.5) is highly variable with respect to distance and season. The kurtosis of the (reflected) distribution also varies widely with the seasons at each station. In general, however, the kurtosis is higher in the summer months than the winter months, suggesting a broader spread of sizes in winter. This contrasts with the pattern shown by *Anapella* group 1.

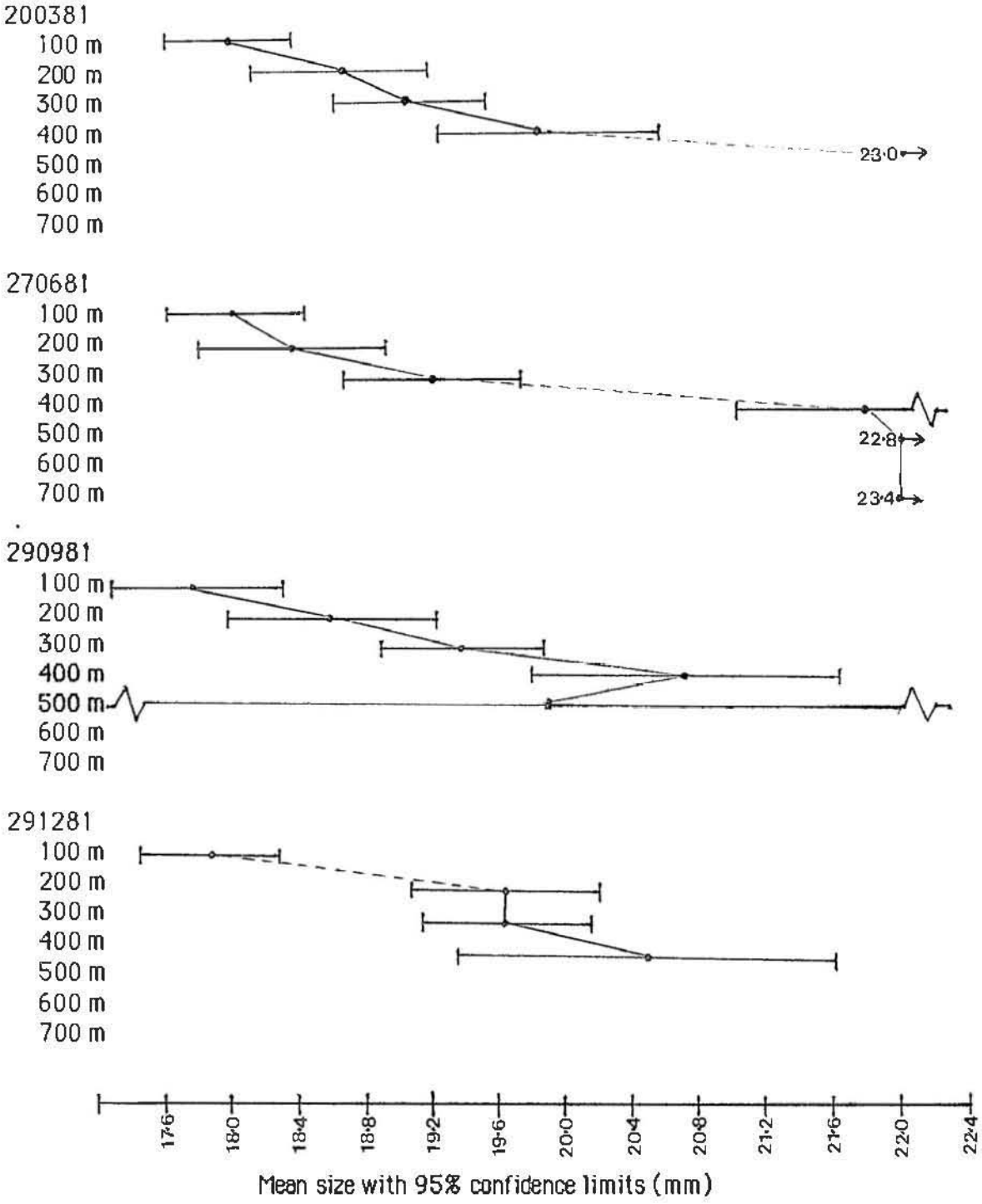


Fig. 3.3 Changes in the mean size of *Anapella* group 2 animals over the transect and through the seasons. Dotted lines indicate significant differences at 5%

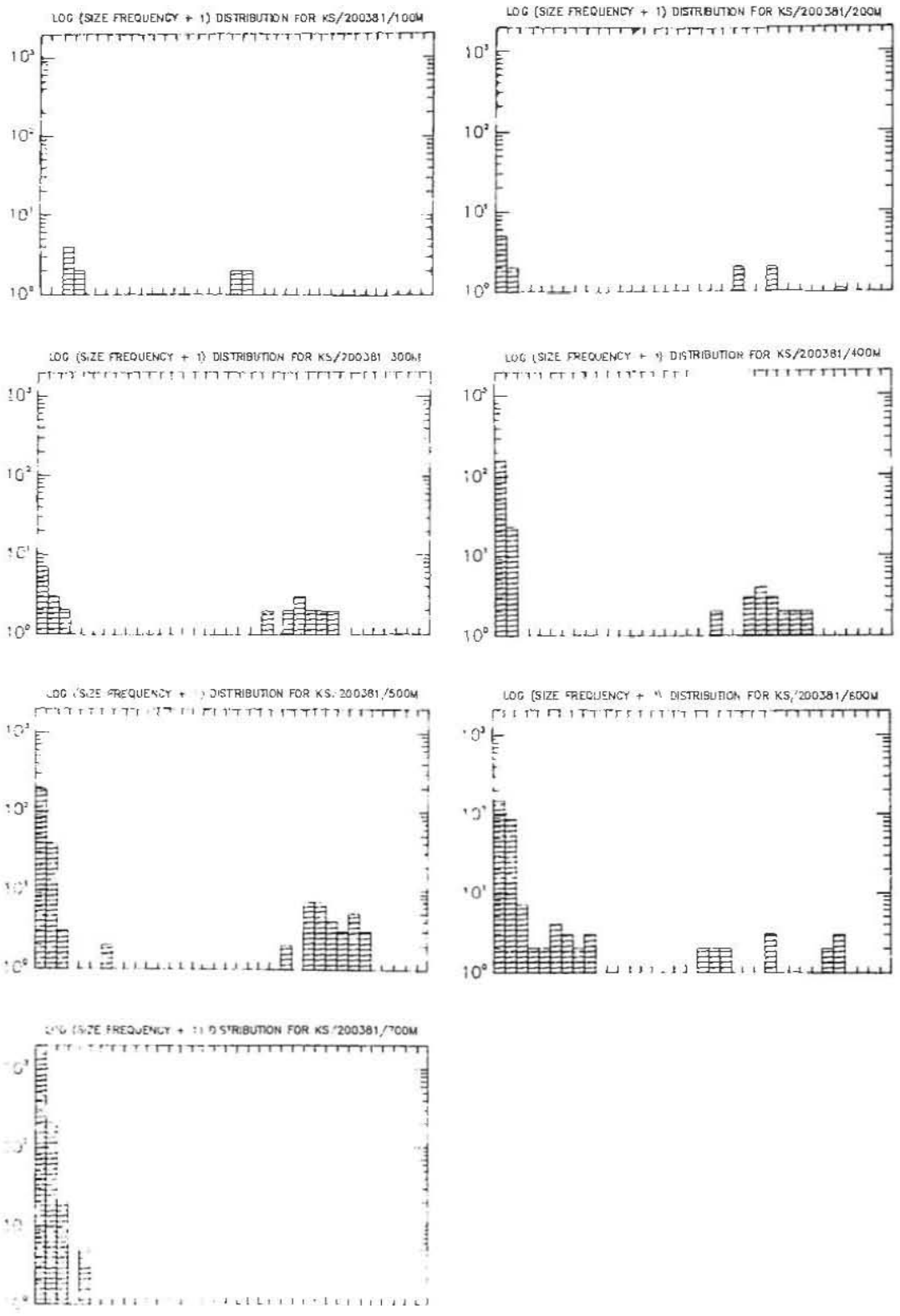


Fig. 3.4 Size frequency distributions of *Katelysia* at dispersion transect stations. Size class axes range from 0 mm to 30+ mm in 1 mm intervals.

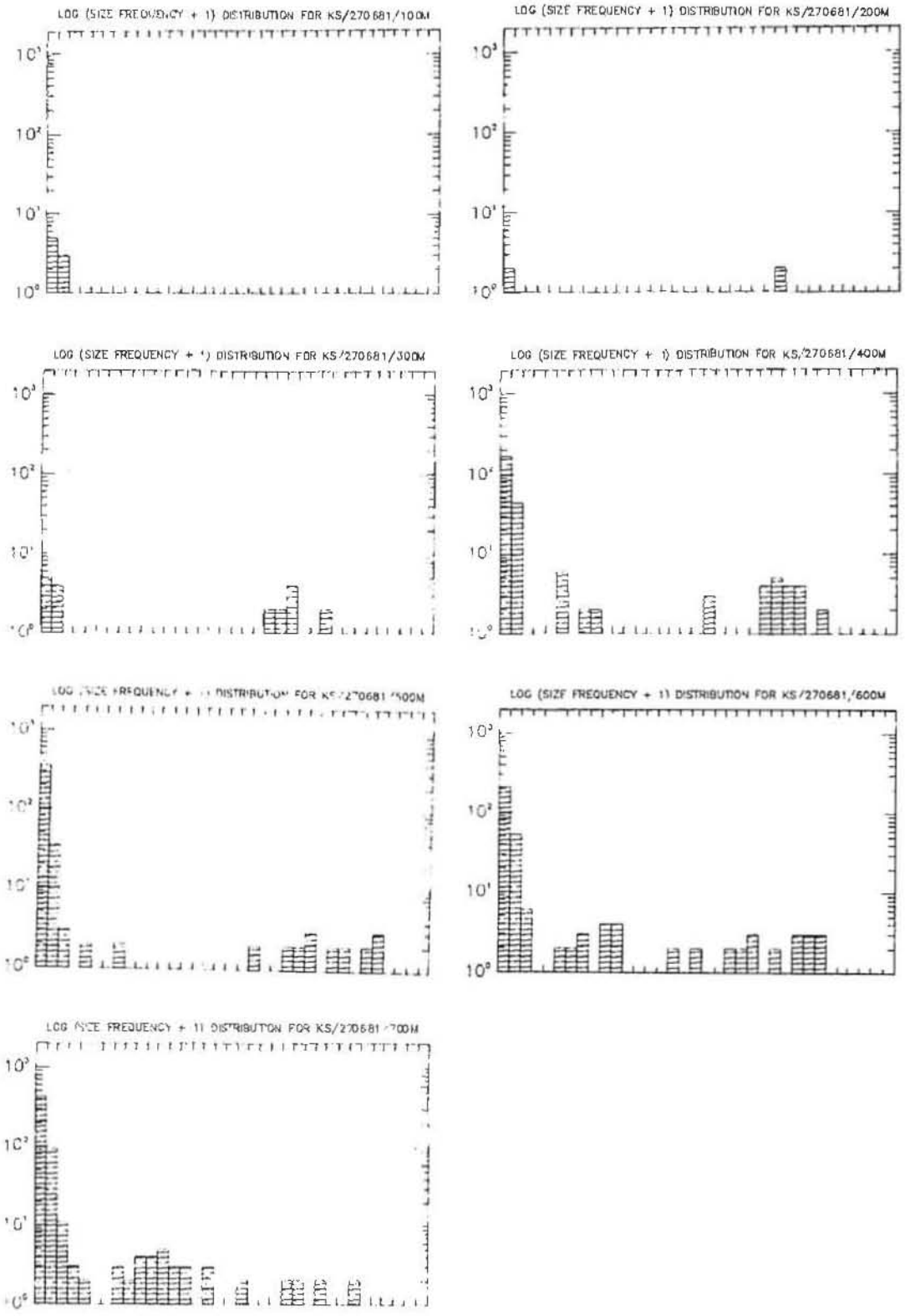


Fig. 3.4 (continued)

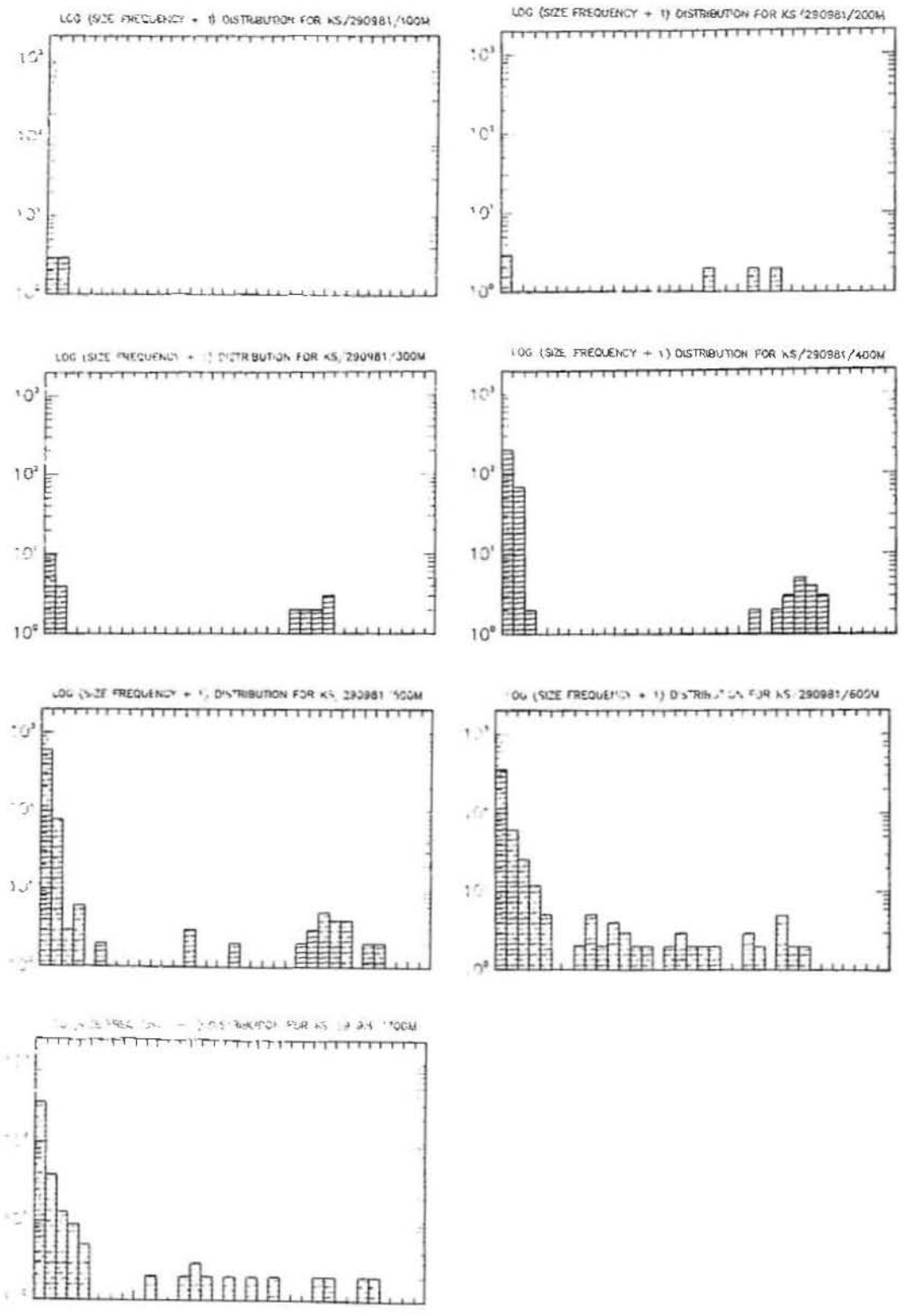
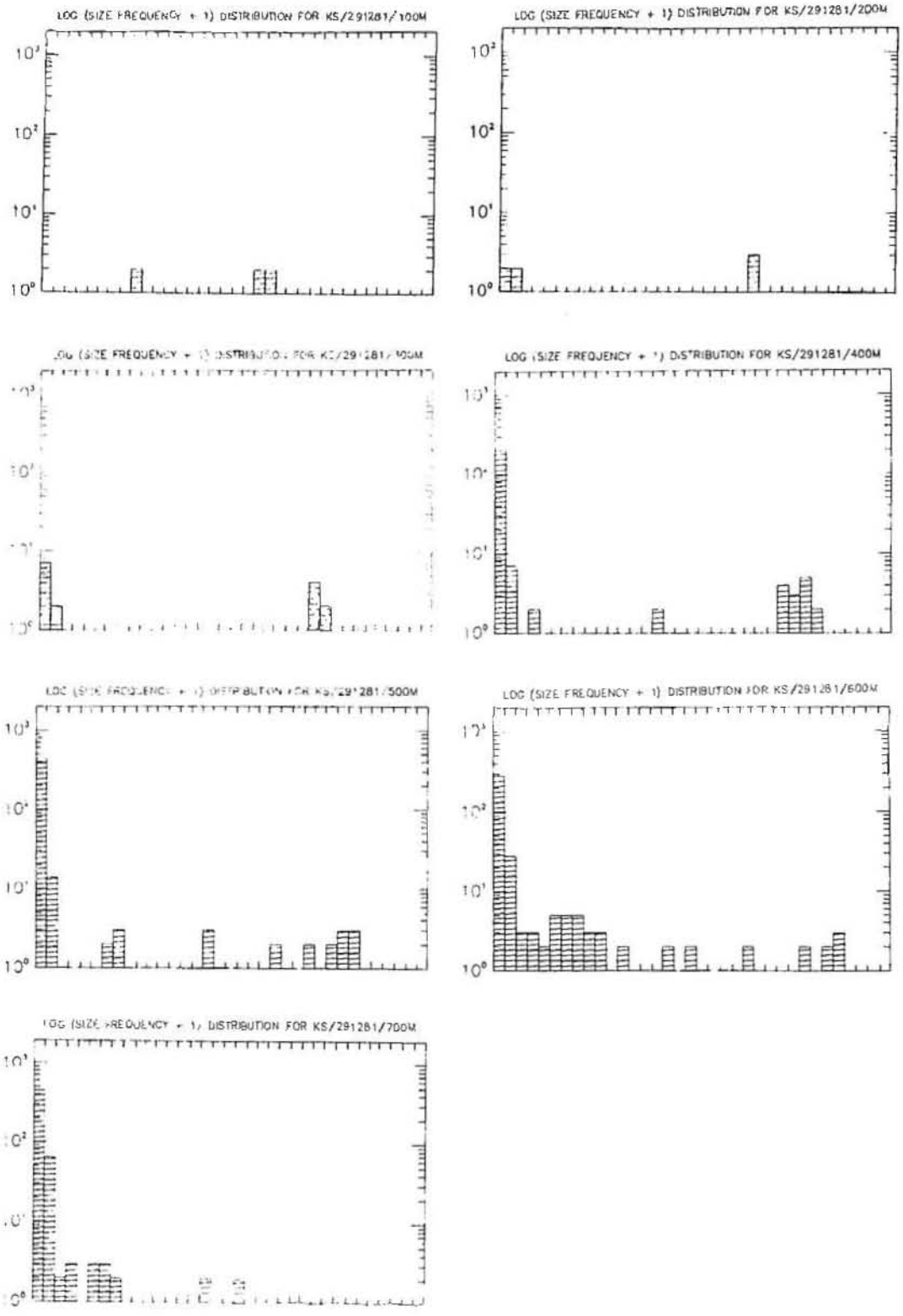


Fig. 3.4 (continued)



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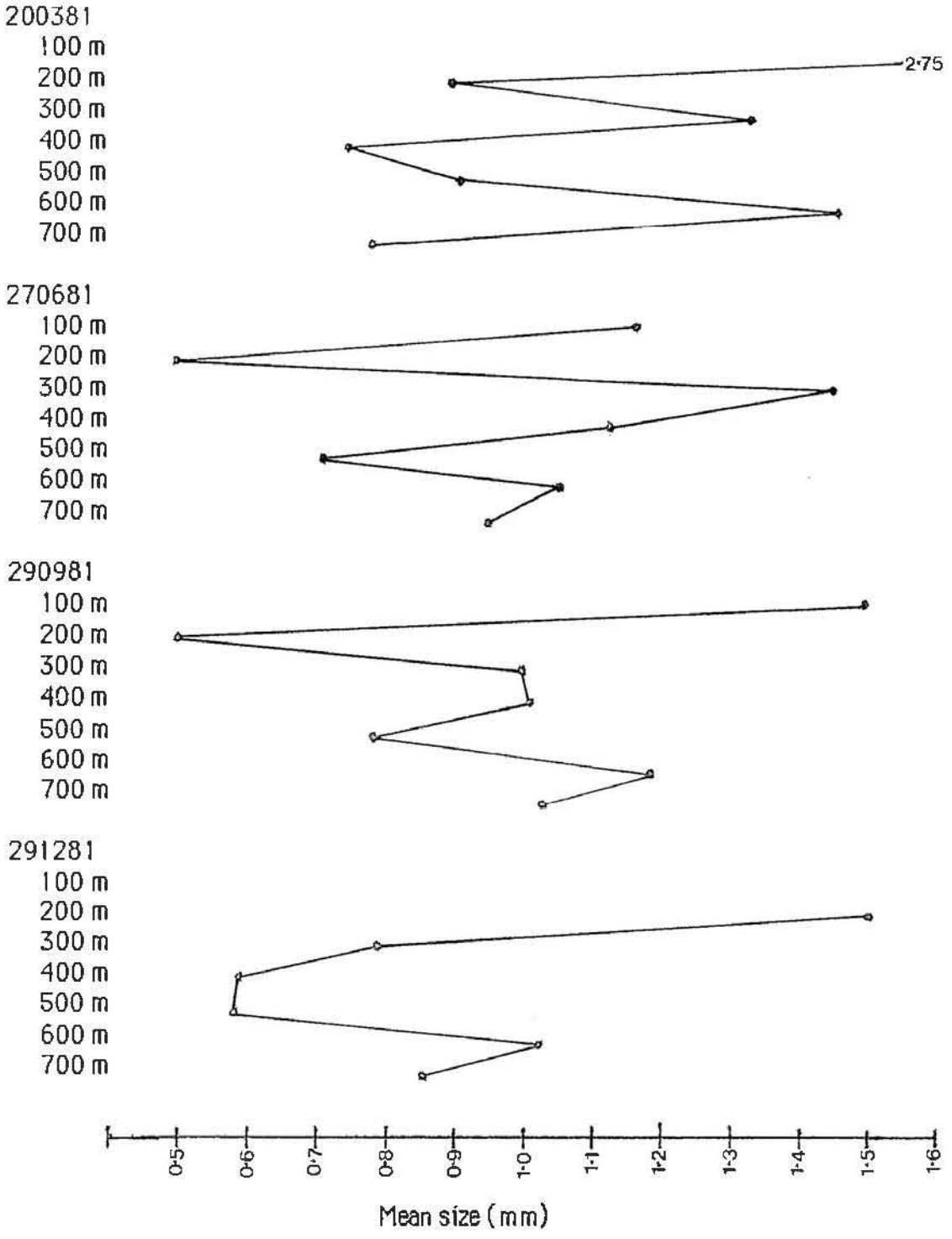


Fig. 3.5 Changes in the mean size of *Kelelysia* group 1 animals over the transect and through the seasons. No confidence limits given due to the non-normality of this group.

The smallest size class (0 mm) is represented throughout the year but is restricted mainly to the lower (400 - 700 m) sections of the beach. On 200381, 0 mm animals are most abundant at 700 m although in that season numbers are low elsewhere. From 200381 to 290981, numbers increase at all distances, particularly at 500 m. After 290981 there is a reduction in numbers throughout the beach.

Katelysia, therefore, shows an up-beach wave of 0 mm animals settling over the winter months similar to that of *Anapella*. In contrast to *Anapella*, however, the lower end of the wave (700 m for *Katelysia*) shows a marked increase in abundance on 200381 and also varies considerably with the seasons. Also, 0 mm *Katelysia* do not reach their maximum abundance until 290981, while *Anapella* 0 mm abundances reach a maximum by 270681 and remain high through to 290981. As with *Anapella*, there is a fairly constant relative abundance of 0 mm *Katelysia* at the lower end of the zone of distribution.

Group 2 (7 - 17 mm)

This group is poorly represented on 200381 but reaches maximum abundance on 270681 before declining through 290981 and 291281. At all times it is only found at 600 m and 700 m. Mean sizes (Fig. 3.6) are highest on 290981 when they approach the lower limit of group 3. There is a corresponding movement towards negative skewness, suggesting an increased growth rate.

Group 3 (18 - 30+ mm)

Overall, group 3 numbers are lowest on 291281 and highest on 200381. In all seasons except 200381, there is a general increase in abundance from 300 m to 400 m, followed by a decrease to 700 m. On 200381 the numbers increase from 300 m to 500 m before declining.

The mean size of group 3 animals (Fig. 3.7) shows a general increase from 300 m to 500 m in each season. There is then a decline to 600 m, except on 291281 when there is a continued increase. There are 3 major departures from zero skewness. At 300 m there is a strong increase in positive skewness on 291281 due to an absence of large group 3 animals but the low numbers make this unreliable. At both 500 m and 600 m there is an increase in negative skewness throughout the year, with a sharp increase on 291281. On 291281 the overall mean size of group 3 animals increases markedly, after little change throughout the year. It appears, therefore, that group 3 animals have a period of rapid growth from spring to summer.

Summary

As with *Anapella*, there is a wave of up-beach settling of *Katelysia* 0 mm animals

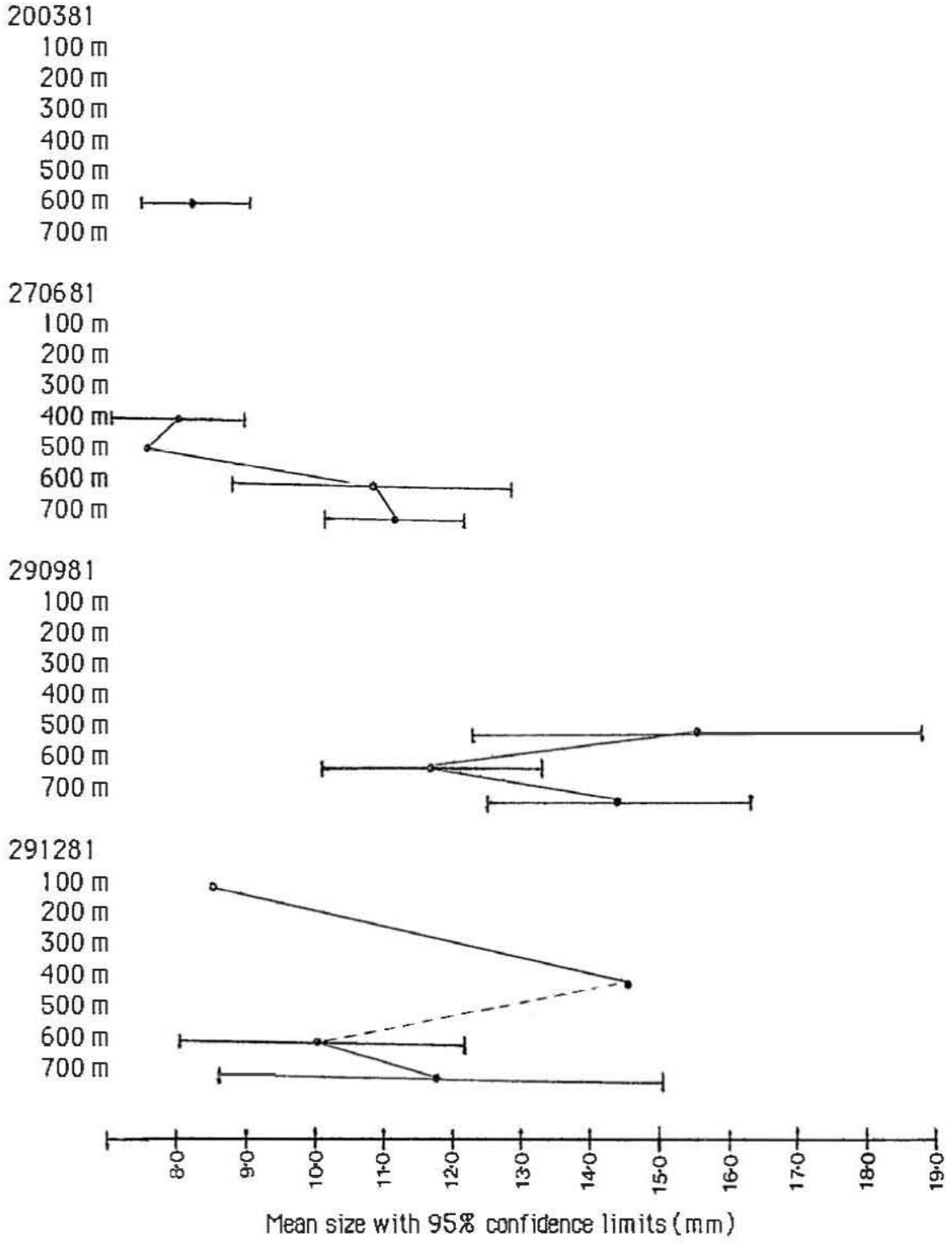


Fig. 3.6 Changes in the mean size of *Katelysia* group 2 animals over the transect and through the seasons. Dotted line indicates significant difference at 5 %.

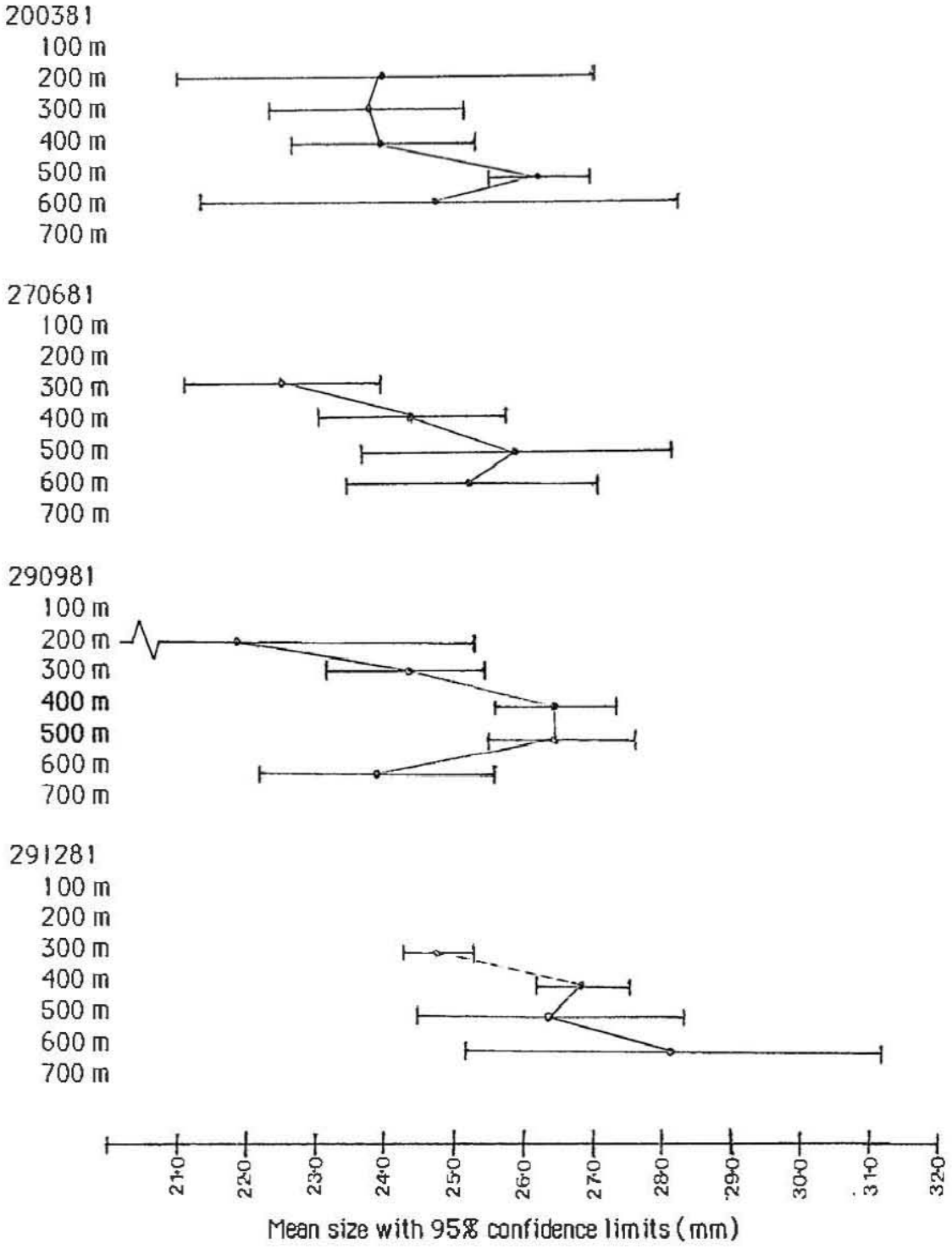


Fig. 3.7 Changes in the mean size of *Katelysia* group 3 animals over the transect and through the seasons. Dotted line indicates significant differences at 5%.

from 200381 through to the peak on 290981 which occurs at least 3 months later than the *Anapella* peak. There is a subsequent pulse of group 2 animals in the 'following' winter and spring which must result from rapid summer/autumn growth of group 1 animals. This, in turn, is followed by an autumn (200382) pulse of group 3 animals, resulting from rapid group 2 growth. The group 3 animals are presumably responsible for the next winter/spring recruitment pulse.

Katelysia and *Anapella* show contrasting rates of growth from group 1 to group 3. *Katelysia* shows a spring peak in recruitment. Rapid summer growth allows those group 1 animals to enter group 2 by the following winter. Subsequent rapid summer growth results in those group 2 animals reaching group 3 by autumn. There is thus approximately 18 months between the settlement of an 0 mm animals and its entering group 3.

Recruitment to the 0 mm size class of *Anapella* reaches a maximum in winter which is maintained through spring. No intermediate size group was detected, although small group 2 animals are most abundant on 200381. Rapid summer growth of the winter group 1 animals leads to them entering group 2 during autumn. The duration of group 1 in *Anapella* is approximately 6 months.

3.3.3 *Soletellina*

The size frequency distribution of *Soletellina* (Fig. 3.8) was separated visually into two groups:

Group 1 (0 mm)

This group is generally restricted to areas below 300 m. Over winter and spring there is a wave of recruitmnent moving up the beach from 700 m, with numbers reaching a maximum on 290981 before dropping from 290981 through 291281 to 200382. The class is represented throughout the year.

Group 2 (1 - 6+ mm)

Group 2 shows little change in mean size (Fig. 3.9) throughout the year, except at 600 m on 290981, when there is a marked increase. Overall numbers are greatest on 270681 and 290981 but the increase is only slight.

The *Soletellina* population appears to exhibit continuous settling of 0 mm animals below 300 m, with maximum numbers occurring in winter. These animals grow to enter group 2 by the following winter/spring.

3.3.4 *Wallucina*

The size frequency distribution of *Wallucina* (Fig. 3.10) can be approximated by a normal curve. Animals of the 0 mm size class are rare and the size frequency distribution

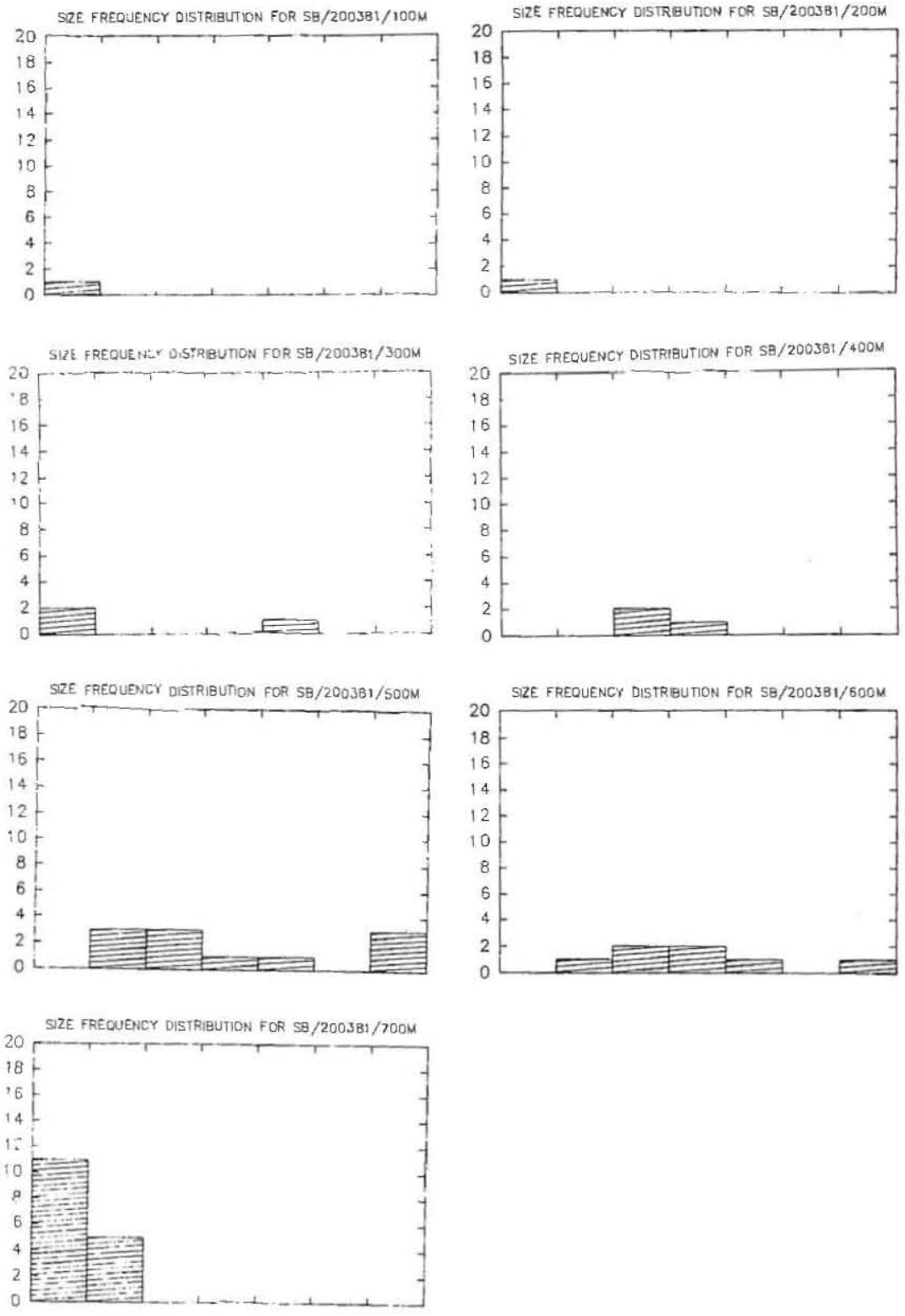


Fig. 3.8 Size frequency distributions of *Soletellina* at dispersion transect stations. Size class axes range from 0 mm to 6+ mm in 1 mm intervals.

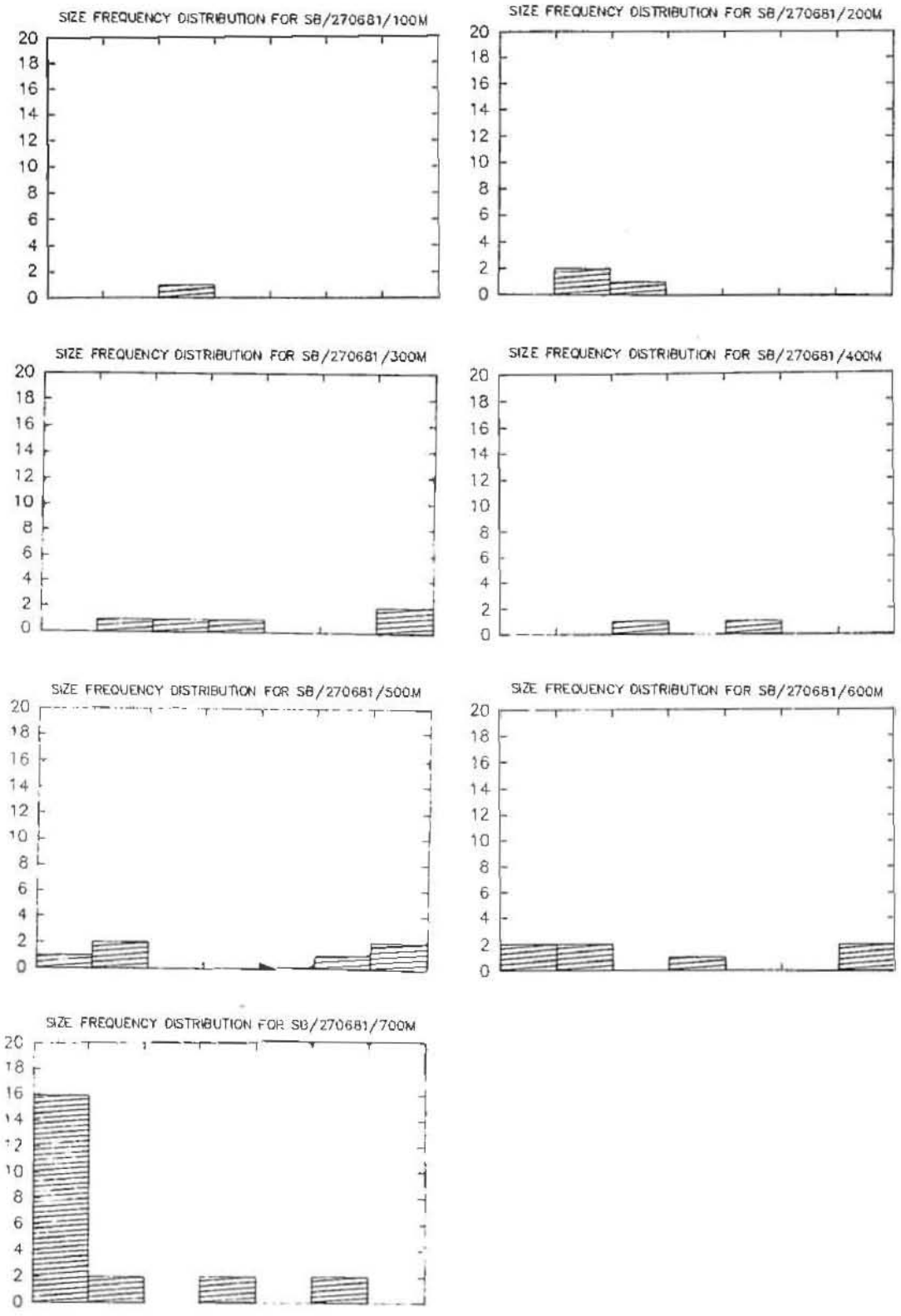


Fig. 3.8 (continued)

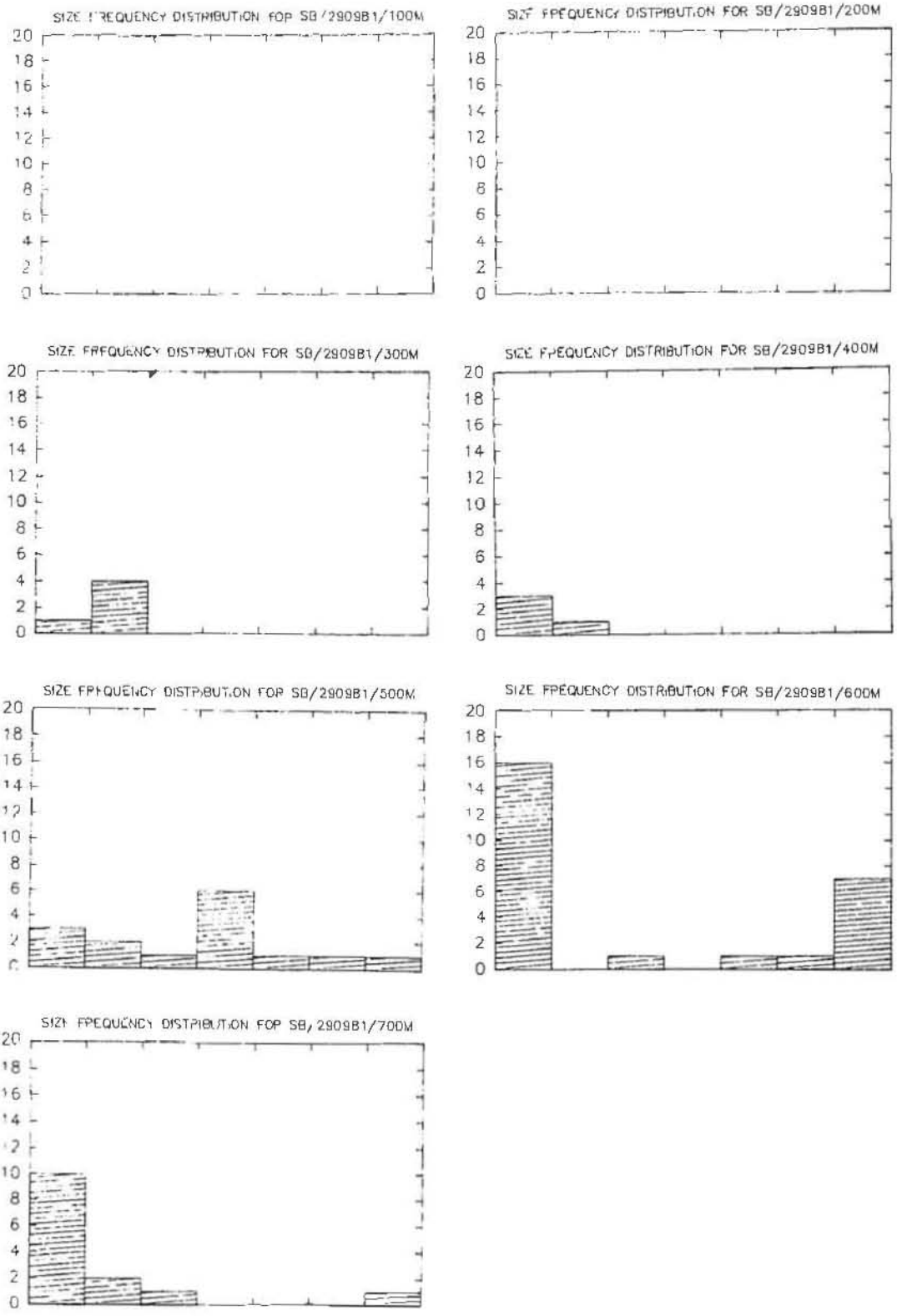


Fig. 3.8 (continued)

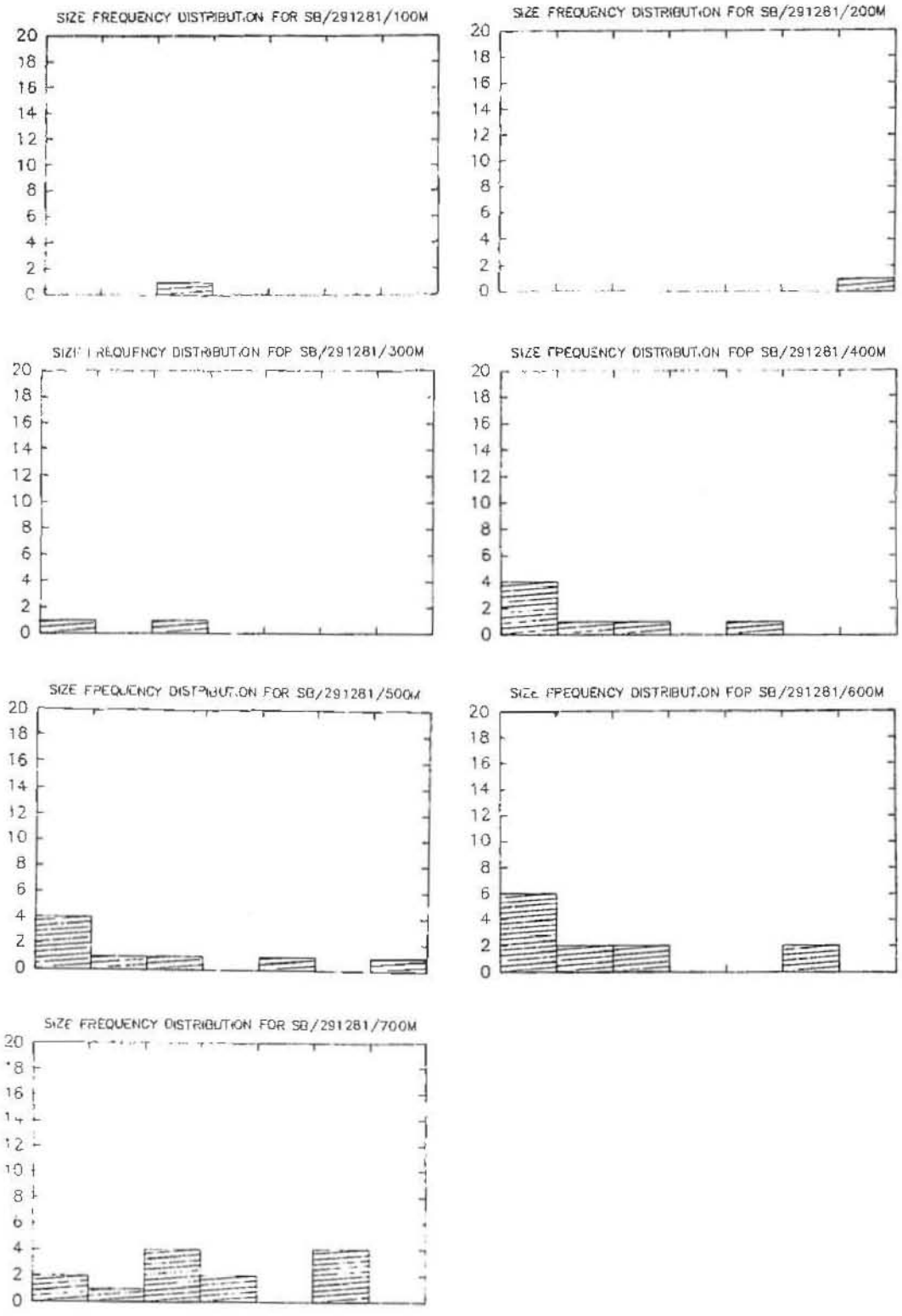


Fig. 3.8 (continued)

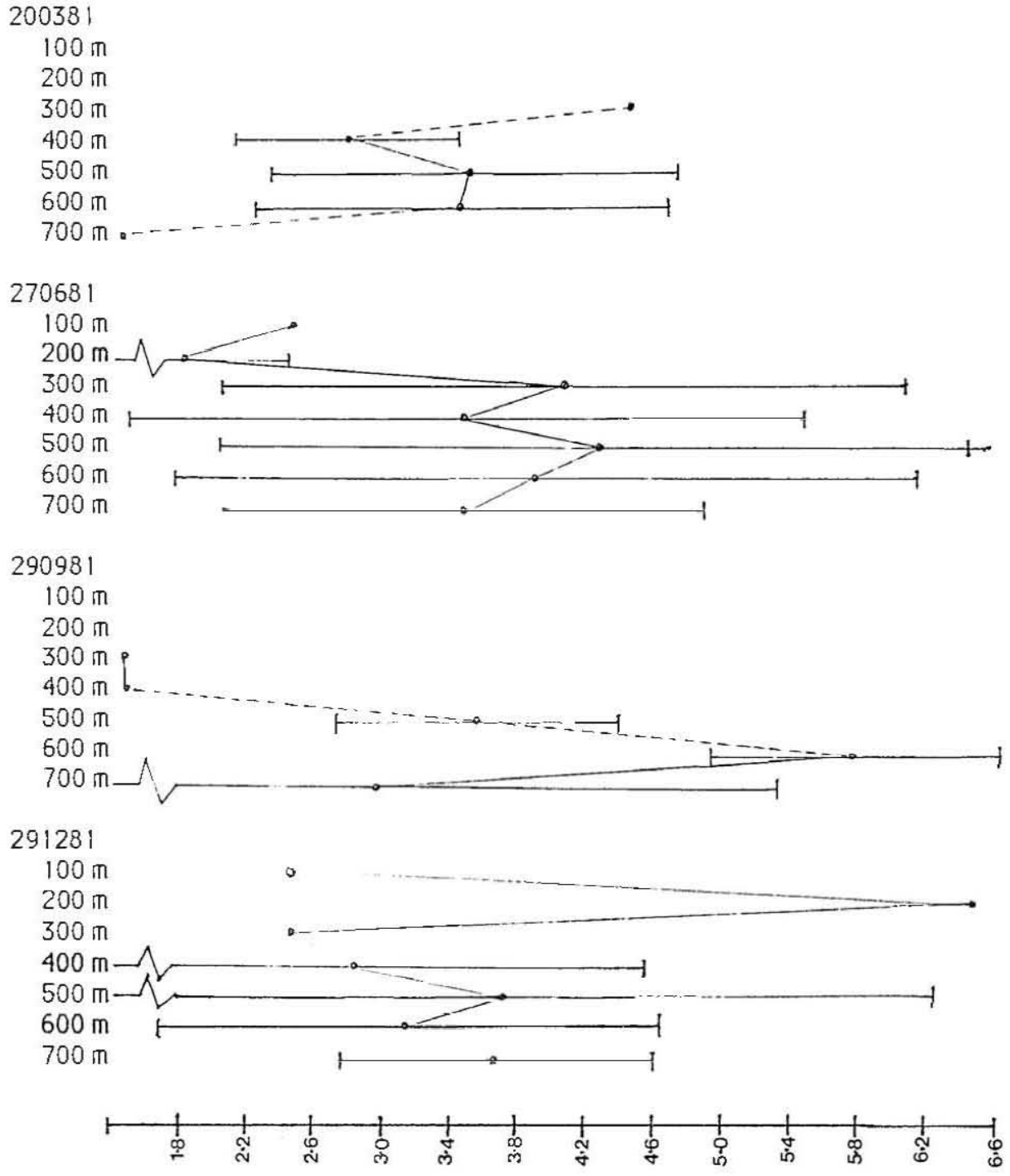


Fig. 3.9 Changes in the mean size of *Soletellina* group 2 animals over the transect and through the seasons. Dotted lines indicate significant differences at 5%.

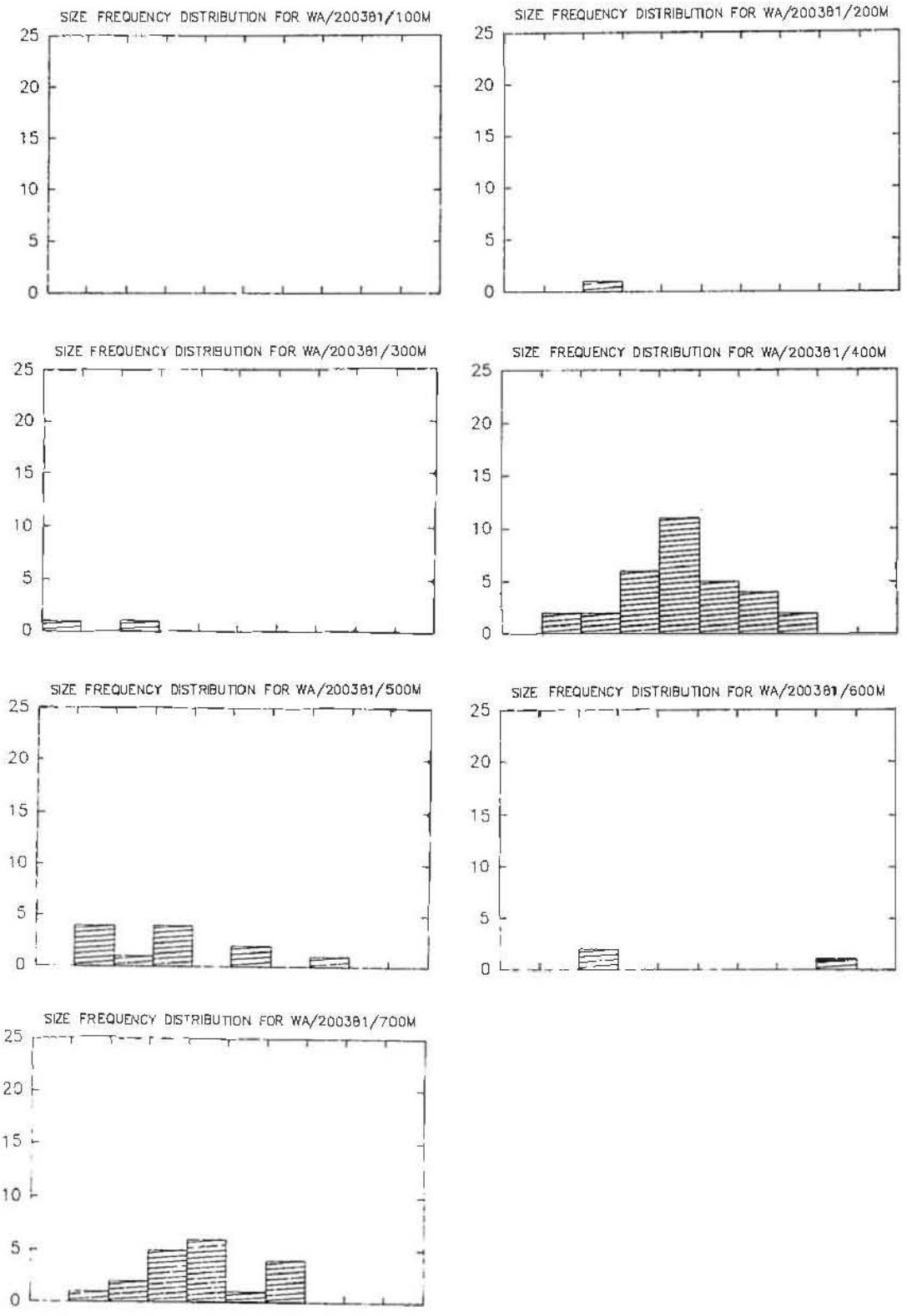


Fig. 3.10 Size frequency distributions of *Wallucina* at dispersion transect stations. Size class axes range from 0 mm to 8+ mm in 1 mm intervals.

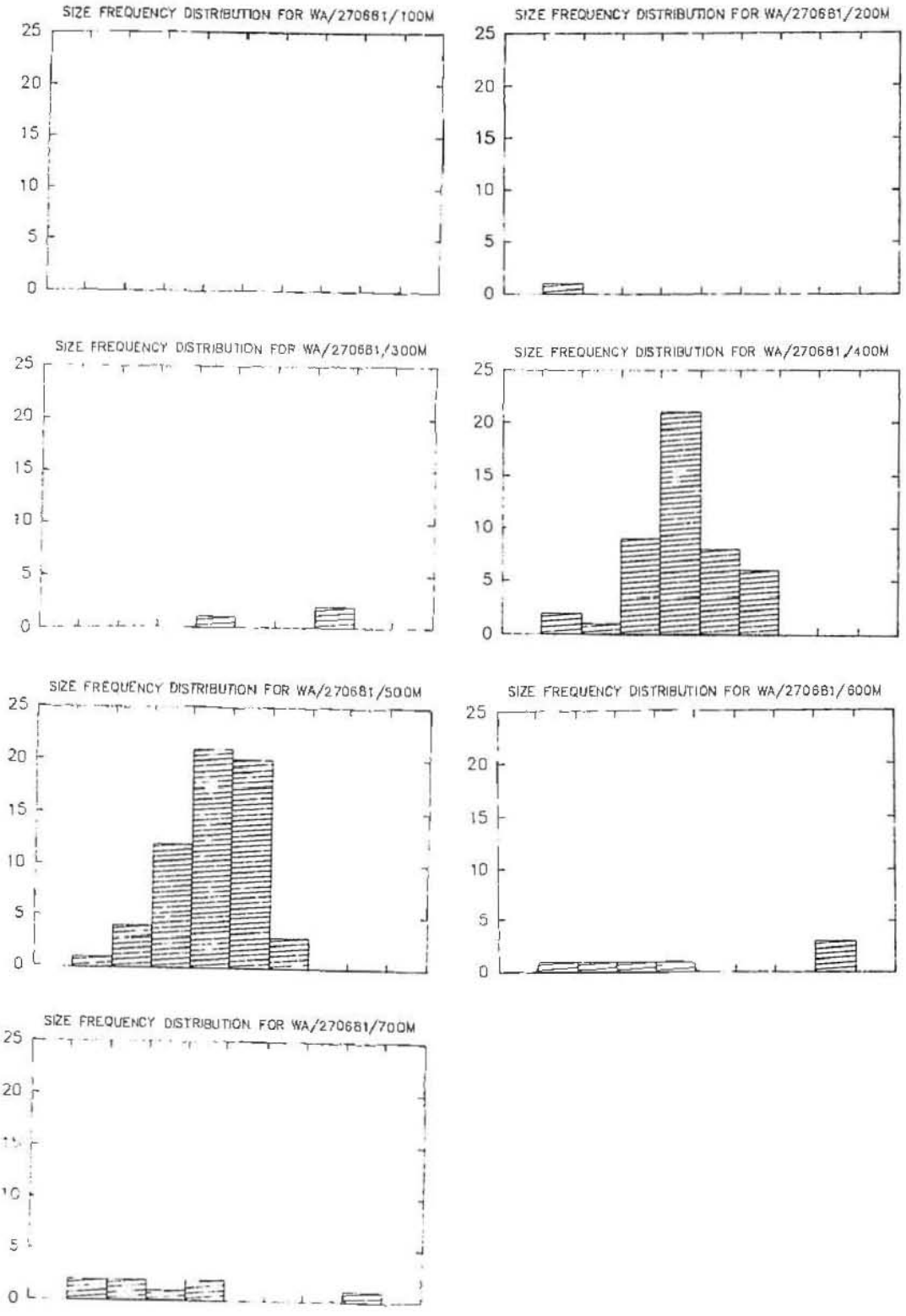


Fig. 3.10 (continued)

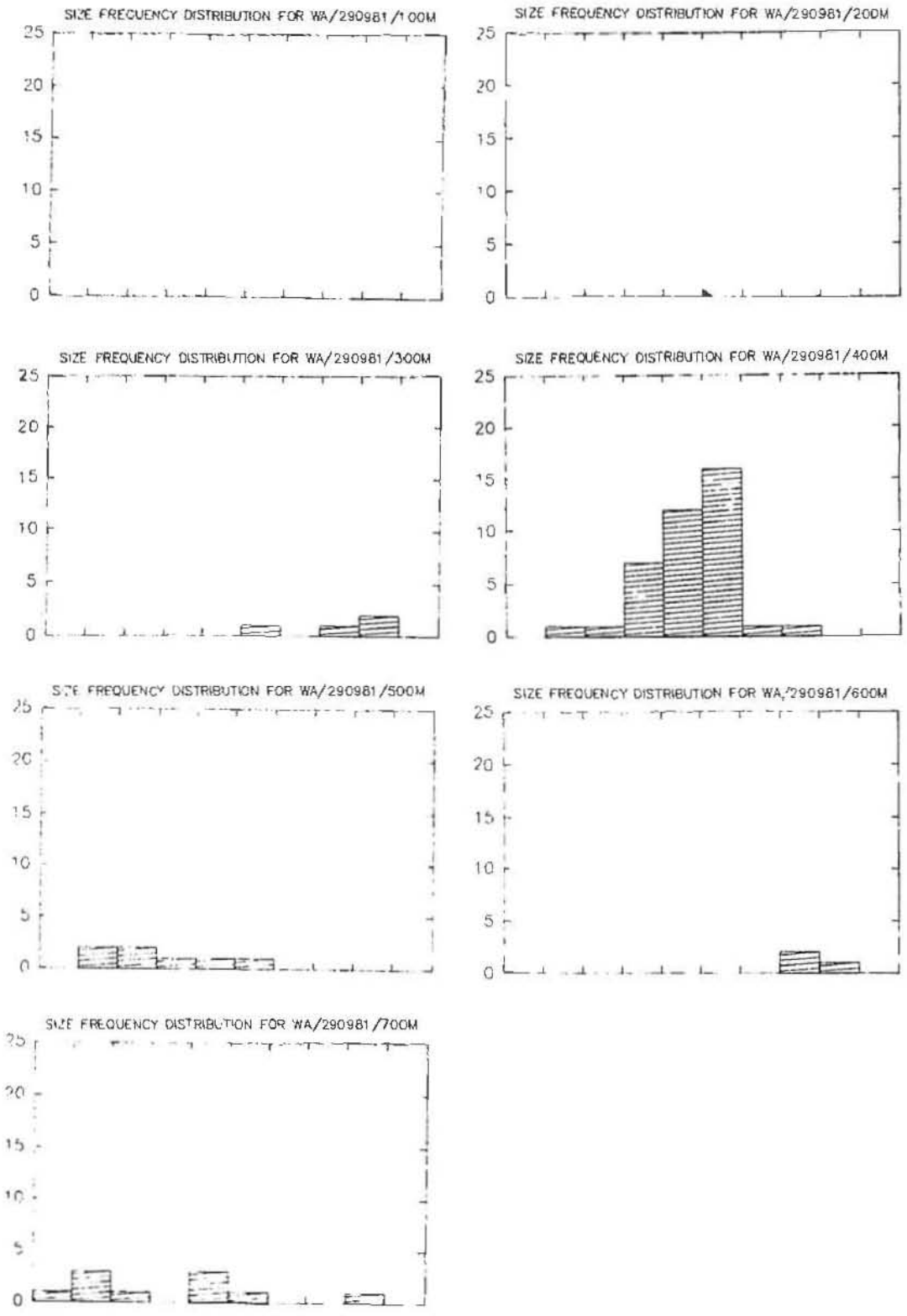


Fig. 3.10 (continued)

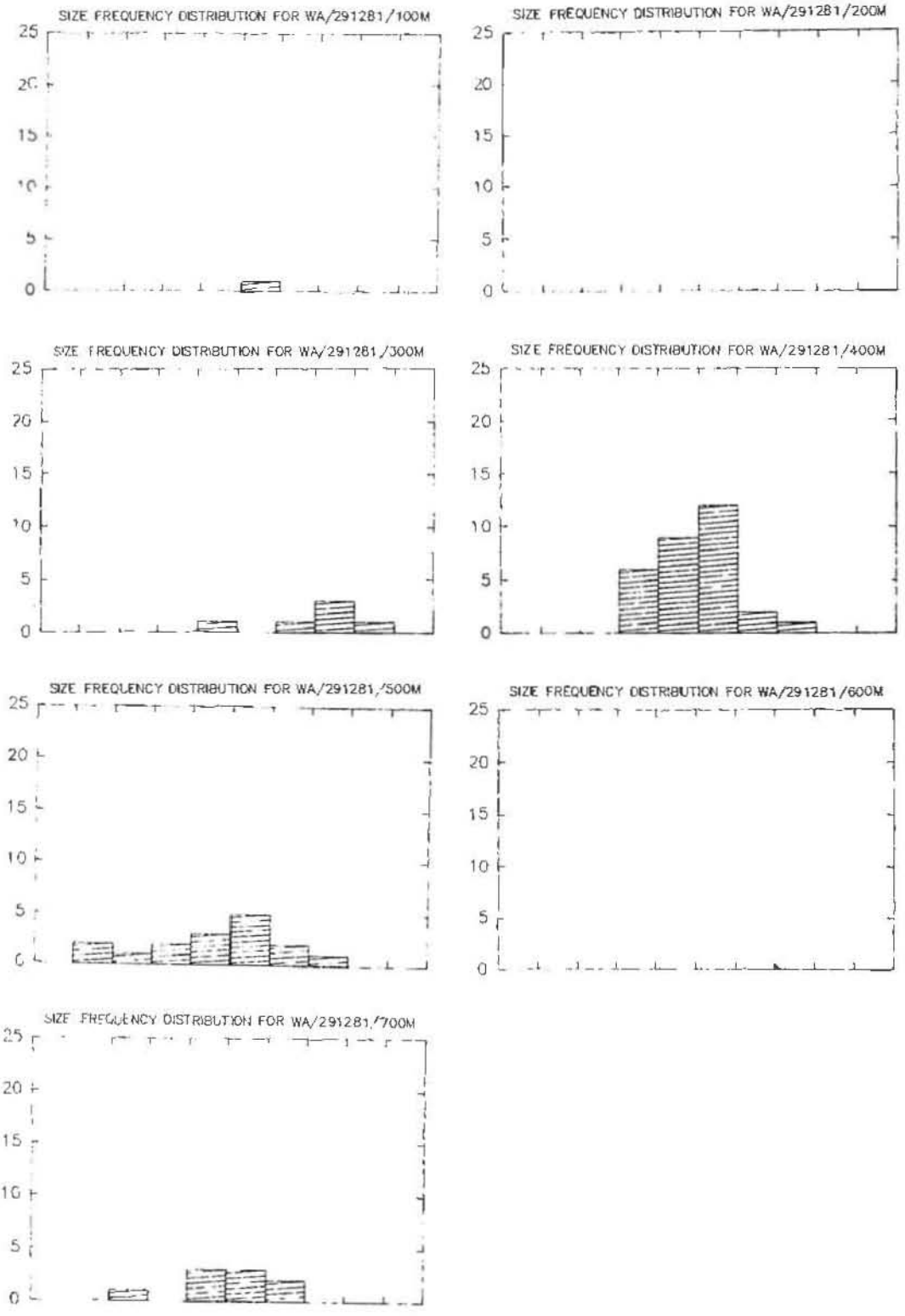


Fig. 3.10 (continued)

was treated as a single group.

The mean size of *Wallucina* (Fig. 3.11) is highly variable with respect to both season and distance. The variations, however, are not statistically significant except at 300 m on 290981 and 291281 when there is a marked increase.

Wallucina is generally restricted to below 300 m, and the numbers at each distance are relatively constant for most of the year. Except on 270681, the abundances increase from 300 m to a peak at 400 m before declining through 500 m and 600 m to low numbers at 700 m. On 270681, the rise from 300 m to 400 m continues to 500 m before the decline. Overall abundance is greatest on this date. The lack of 0 mm animals suggests that recruitment occurs between the autumn and winter. Numbers then decline as the animals grow over spring and summer.

3.3.5 *Hydrococcus*

Hydrococcus (Fig. 3.12) was separated into 3 groups. The first and third groups each comprise a single size class, while the second occupies 3. Group 2 can be represented by a normal distribution.

Group 1 (0 mm)

Throughout the year the pattern is for low numbers from 100 m to 500 m, followed by a sharp increase through 600 m to 700 m. Overall numbers are low on 200381, increasing to maximum abundance on 290981 before declining again.

Group 2 (1 - 3 mm)

There is significant variation in the mean size of group 2 (Fig. 3.13) with respect to both distance and season. At 100 m the mean size is low on 291281 (at 200m the mean size is high in the following season) while at 300 m and 400 m the mean size is low on 270681 and 290981. At 500 m and 600 m there is little change in mean size during the year, and at 700 m the mean size is high on 291281.

These changes are accompanied by changes in the skewness of group 2. At 100 m and 200 m skewness is close to zero until 291281 when there is positive skewness. There is little deviation from zero skewness at 300 m during the year. At 400 m skewness is negligible on 200381 but increases to high positive skewness on 270681 which increases further on 290981 before falling towards zero on 291281. At 500 m, 600 m and 700 m skewness is slightly negative on 200381, becomes positive on 270681, falls to near zero on 290981 and then becomes positive on 291281, particularly at 500 m and only slightly at 700 m.

The positive skewness and decrease in group 2 mean size at 100 m suggests an influx of young animals on 291281. At 200 m there is a similar change in skewness on that date

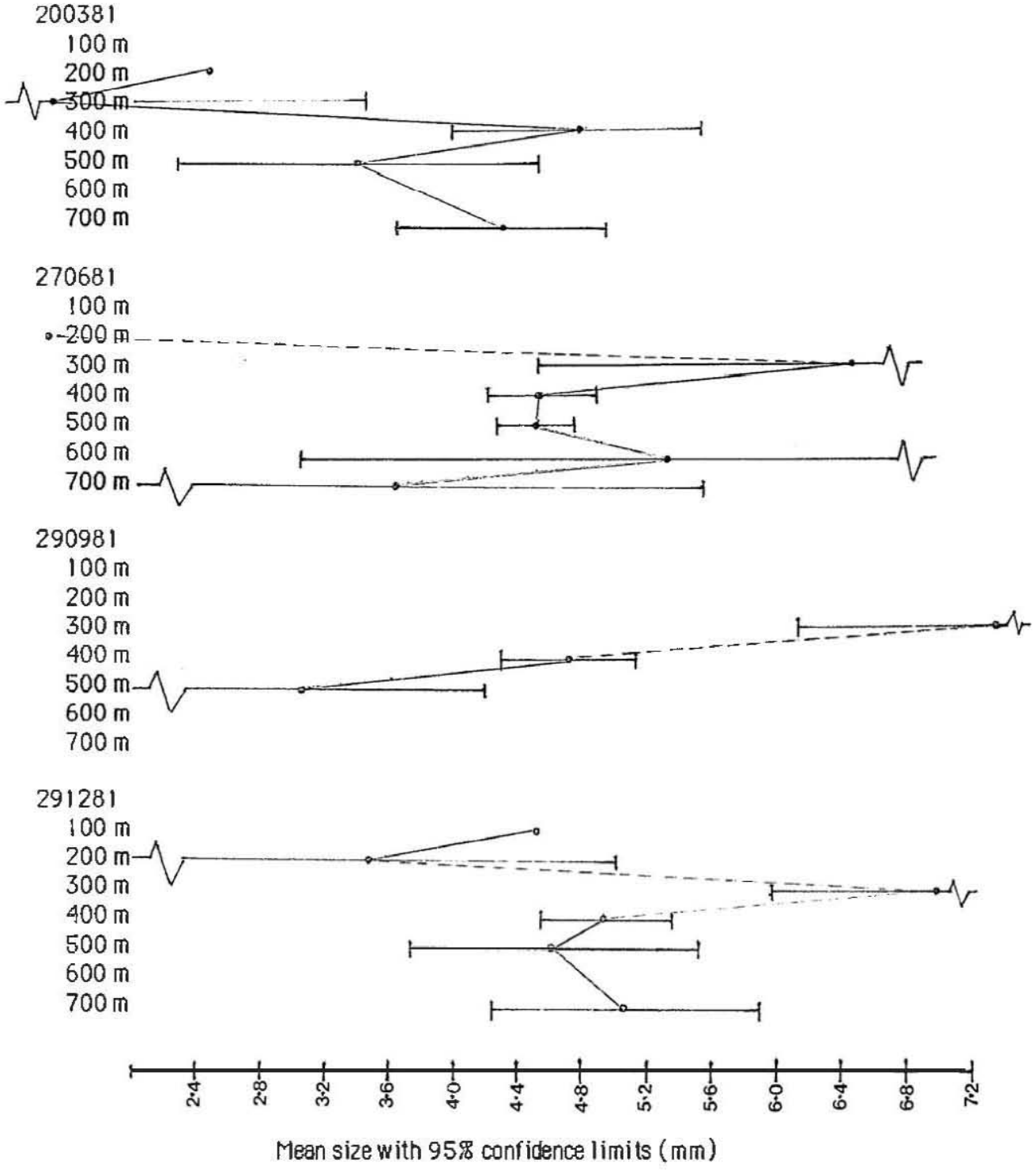


Fig. 3.11 Changes in the mean size of *Wallucina* over the transect and through the seasons. Dotted lines indicate significant differences at 5%

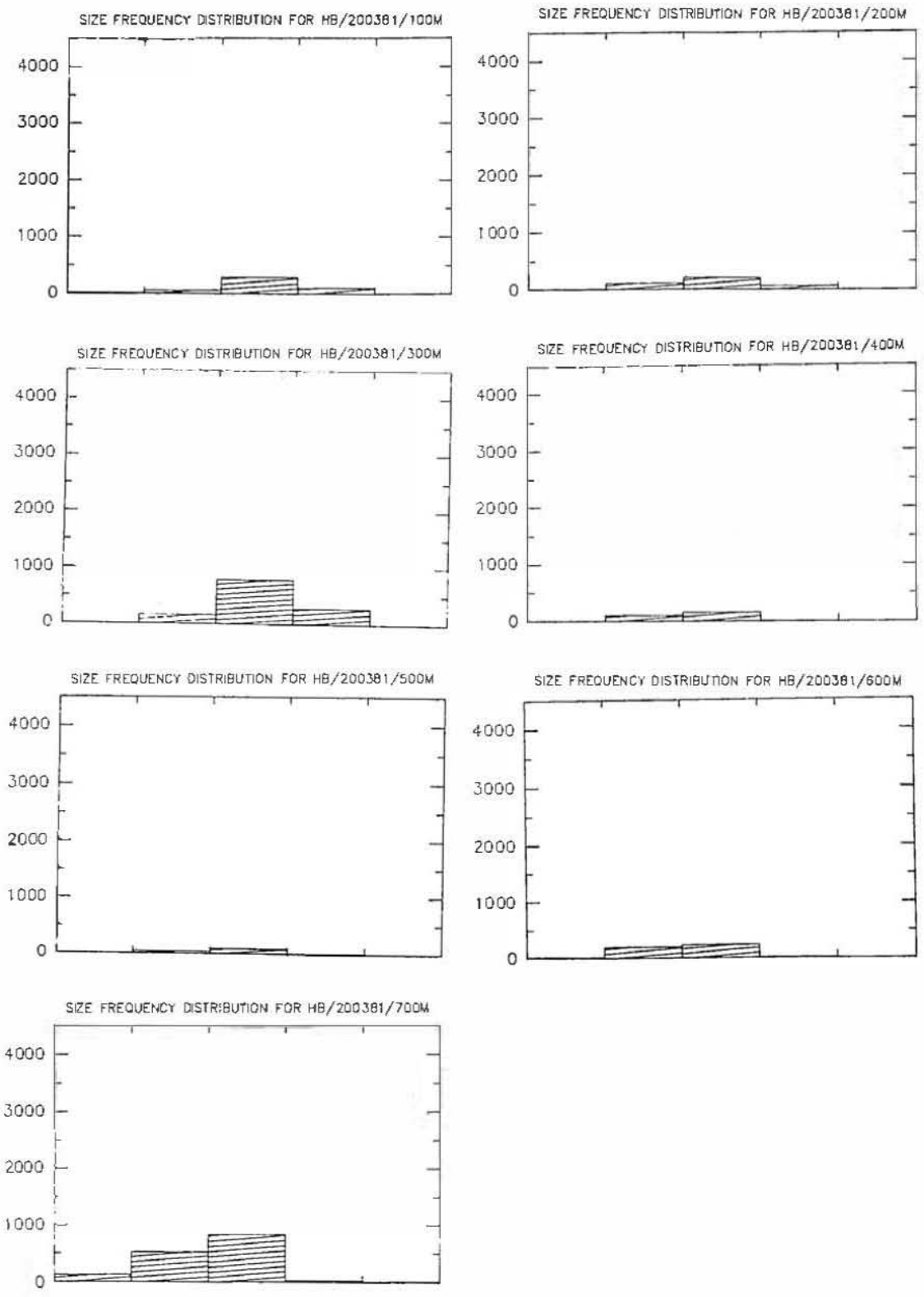


Fig. 3.12 Size frequency distributions of *Hydrococcus* at dispersion transect stations. Size class axes range from 0 mm to 4+ mm in 1 mm intervals.

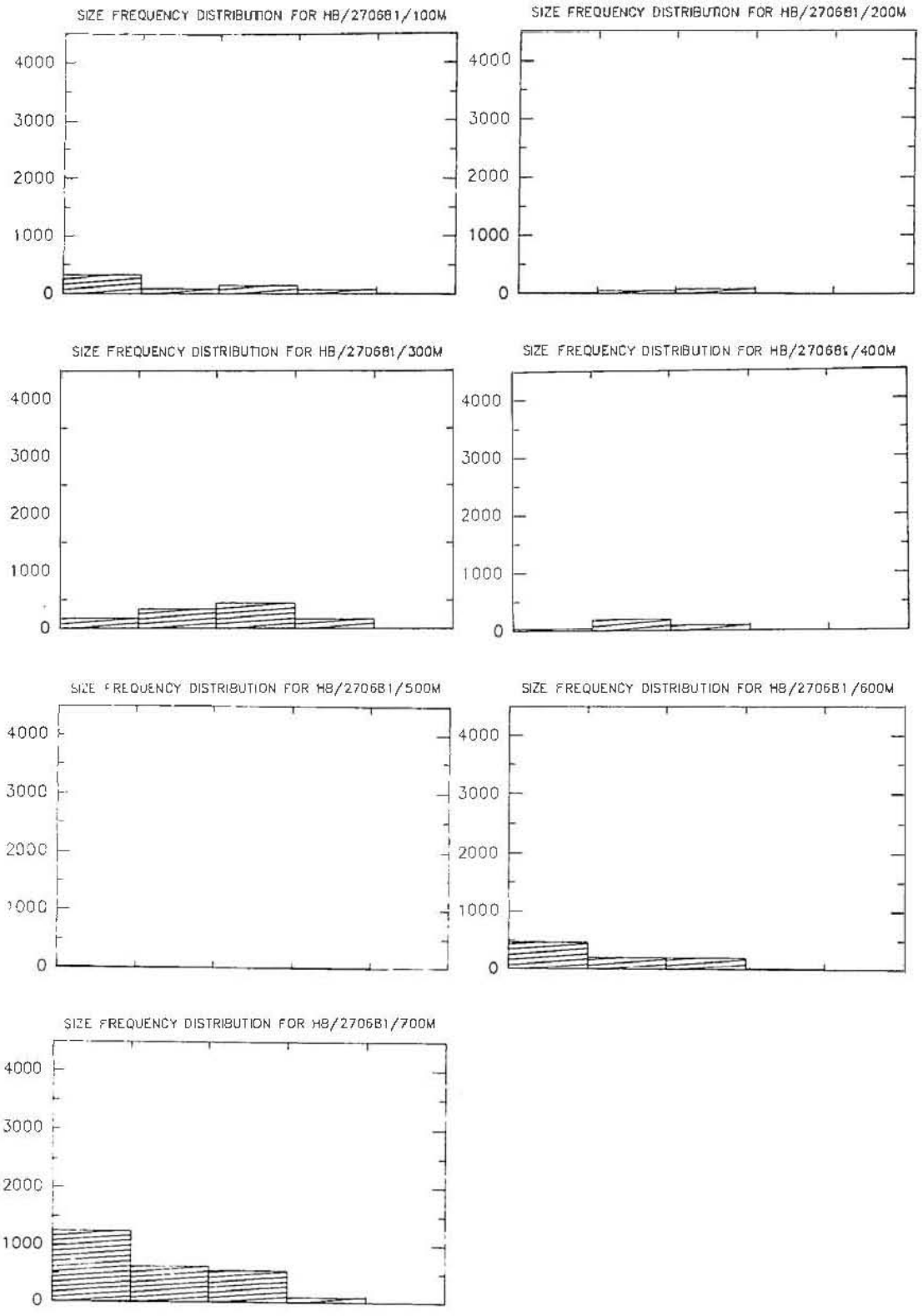


Fig. 3.12 (continued)

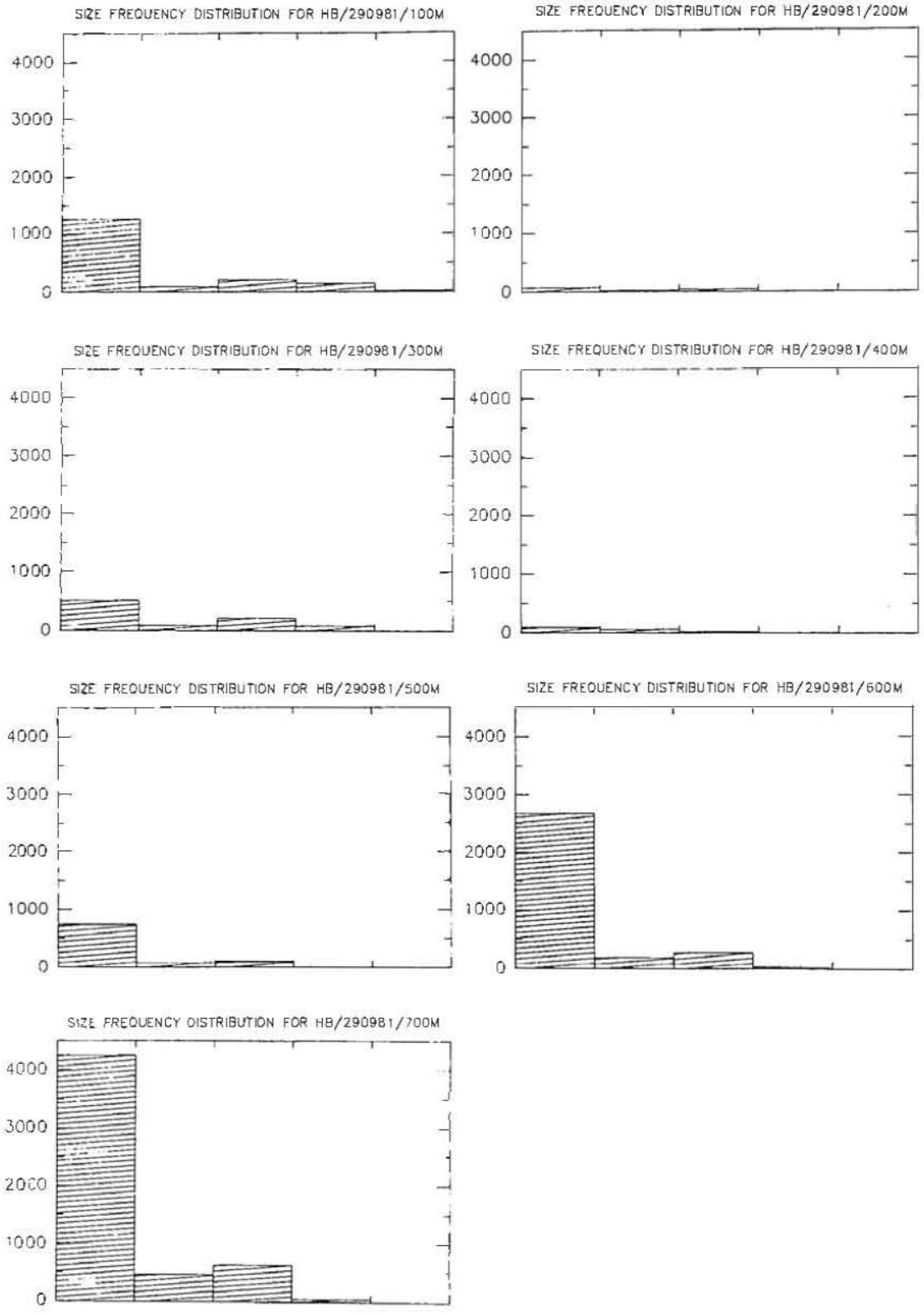


Fig. 3.12 (continued)

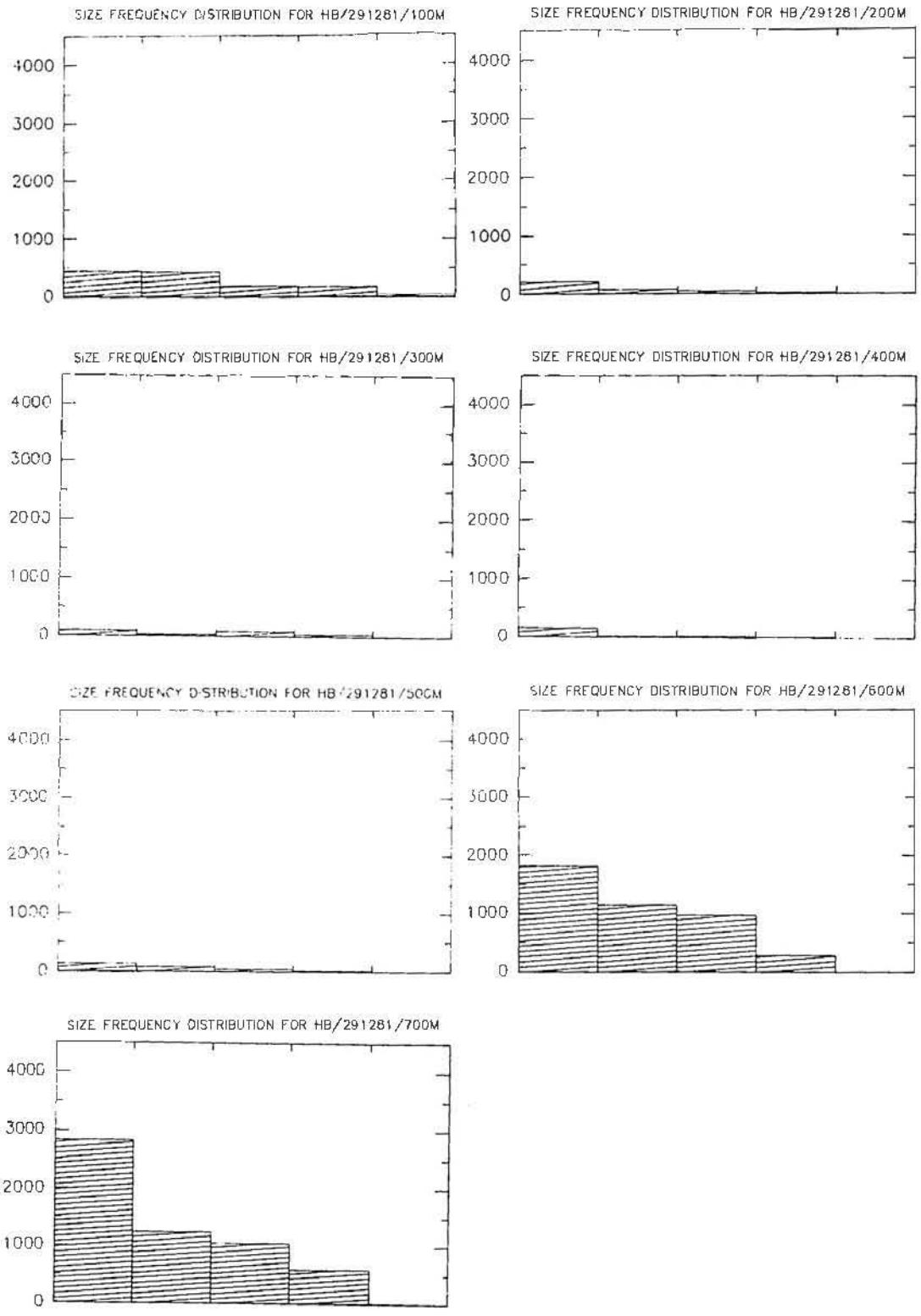


Fig. 3.12 (continued)

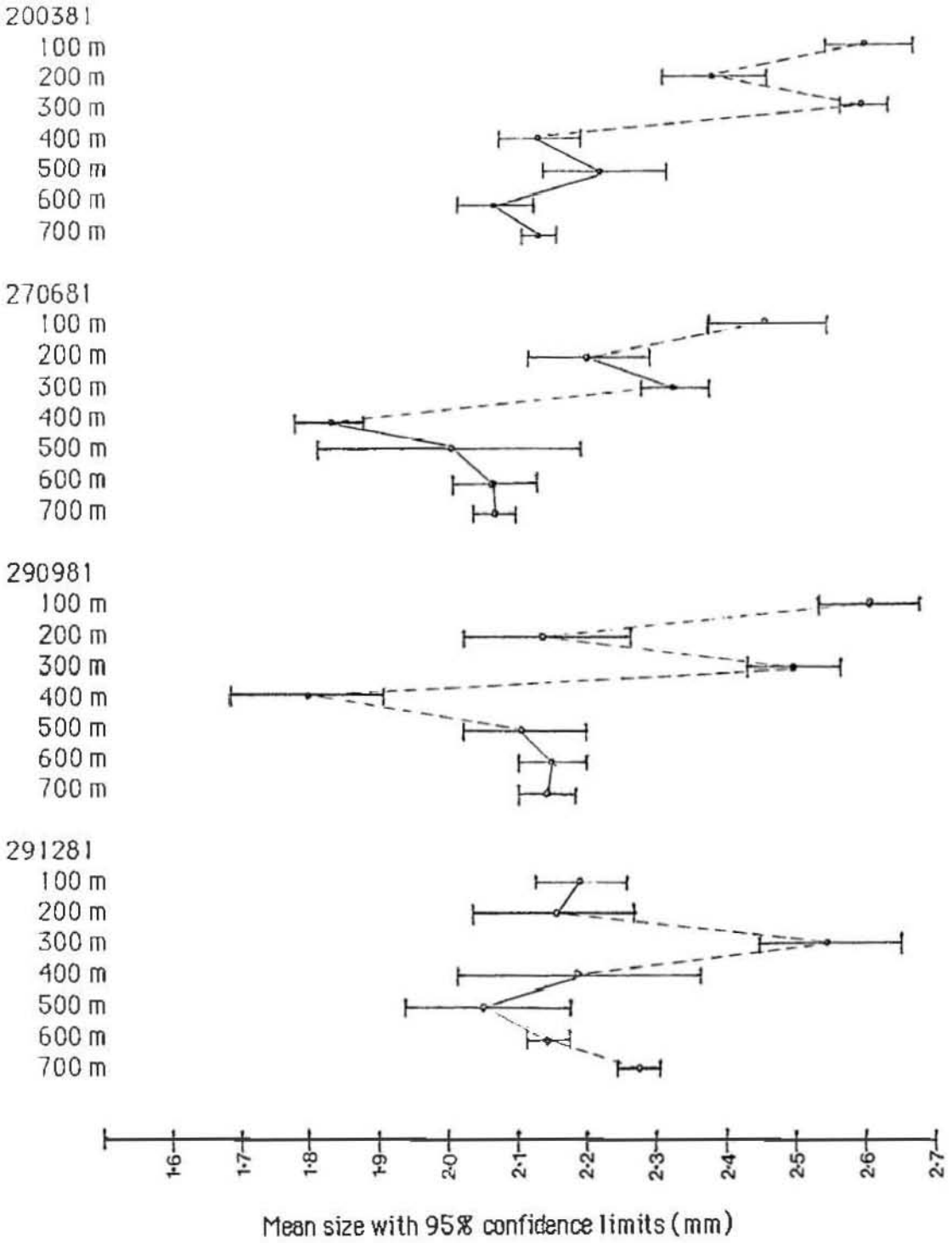


Fig. 3.13 Changes in the mean size of *Hydrococcus* group 2 animals over the transect and through the seasons. Dotted lines indicate significant differences at 5 %

although the influx does not significantly change the mean size. At 300 m the mean size decreases significantly on 270681 and this is accompanied by a slight increase in positive skewness. An influx from group 1 on 270681 and 290981 at 400 m causes a high positive skewness and a significant reduction in mean size. There is an influx of young animals to group 2 on 291281 at 500 m, 600 m and 700 m which is reflected by a shift to positive skewness (slight at 700 m). There is no significant reduction in mean size, however. In fact, there is a significant increase in mean size at 700 m, suggesting the influx to be well advanced on 291281.

At 300 m and 400 m, then, the influx of young animals, as indicated by changes in the mean size and skewness of group 2, is predominantly during the winter and spring. Only at 300 m on 270681, however, is this accompanied by a marked increase in abundance of group 2 animals. Even then, the abundance at 300 m is less than on 200381 (skewness is negligible on 200381).

At all other distances the changes in mean size and skewness suggest the major influx of animals into group 2 to appear on 291281. At 600 m and 700 m there are also marked increases in abundances on that date.

Group 3 (4+ mm)

These animals are restricted to the upper 300 m of the beach. They are found throughout the year but are in relatively low numbers on 200381 and 270681 before abundances increase rapidly through 290981 to 291281.

Summary

Major recruitment of *Hydrococcus* occurs over winter/spring. These animals grow to enter group 2 during spring (300 m, 400 m) or summer (other stations). The increase in abundances of group 3 animals through 290981 to 291281 also suggests spring/summer to be a period of rapid growth.

3.3.6 *Zeacumantus*

The size frequency distribution (Fig. 3.14) was separated into 3 groups:

Group 1 (0 - 1 mm)

There are significant changes in the mean size of group 1 (Fig. 3.15) throughout the year. At 100 m and 200 m the mean size is greater on 291281 than on 200381, and on the latter date the class has a greater size than on 270681 and 290981. At 300 m group 1 animals are slightly larger on 200381 and 291281 than on 270681 and 290981. There is little change in size through the year at 400 m, except for a small increase on 291281.

The high mean size at 100 m on 291281 is accompanied by negative skewness,

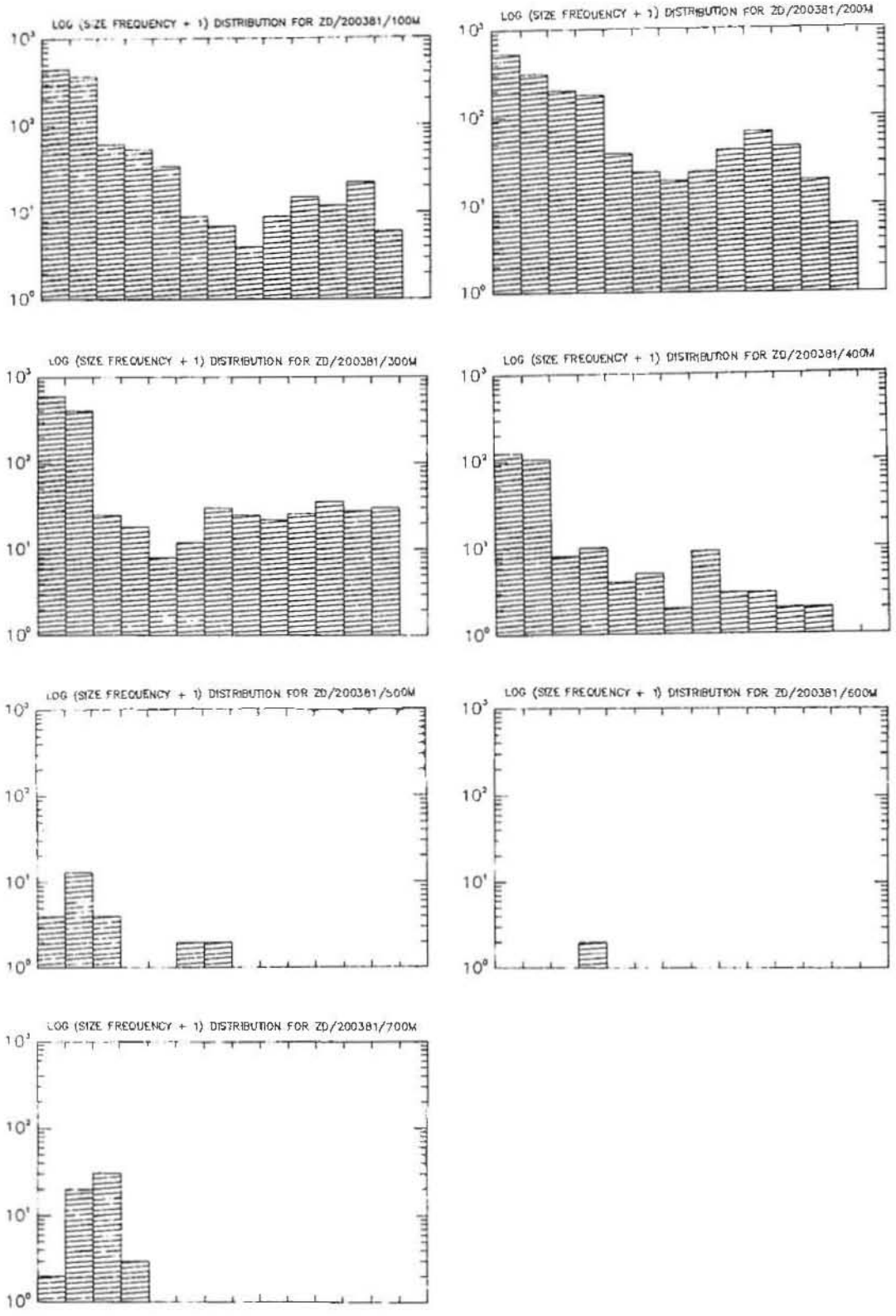


Fig. 3.14 Size frequency distributions of *Zeacumantus* at dispersion transect stations. Size class axes range from 0 mm to 12+ mm in 1 mm intervals.

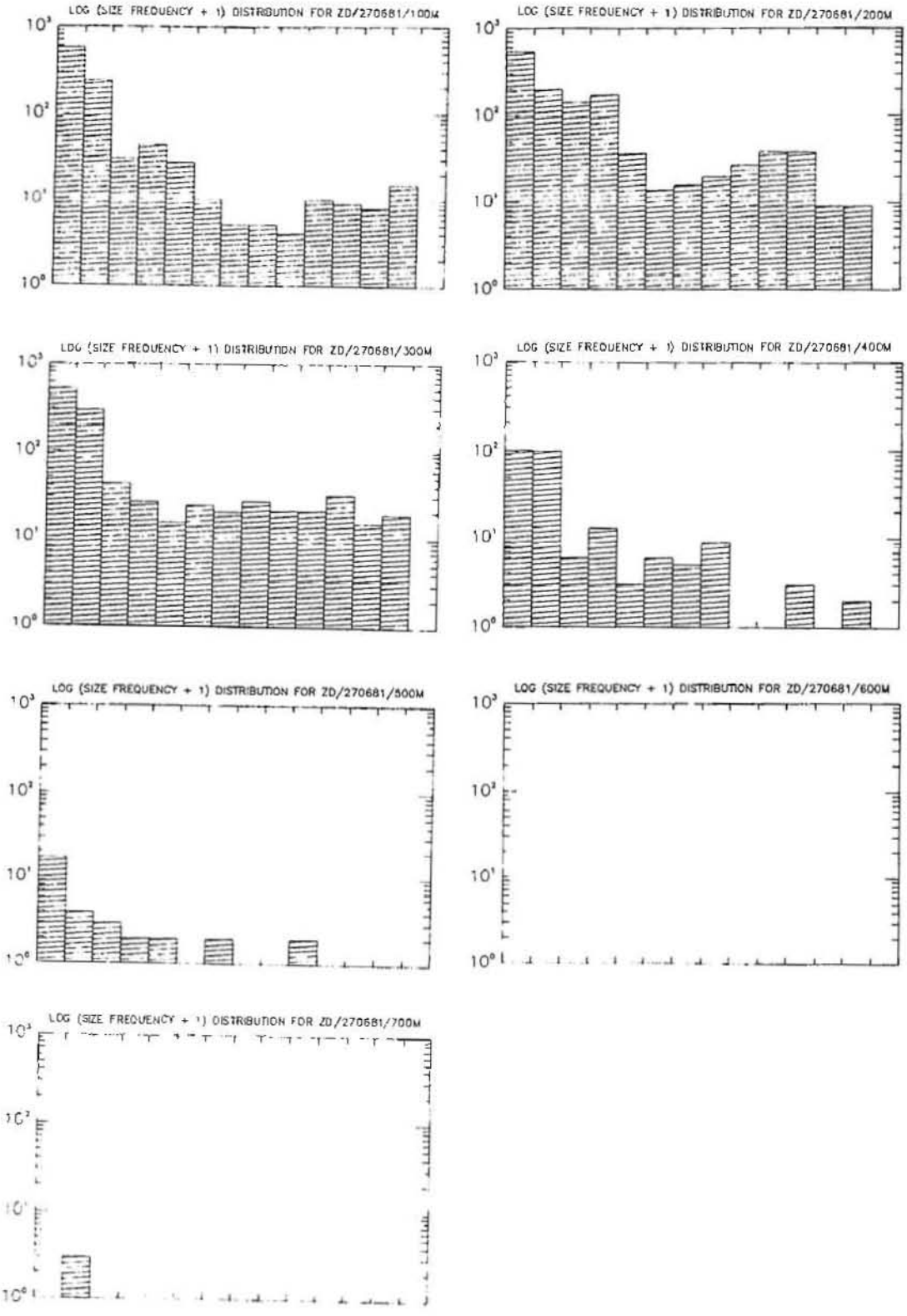
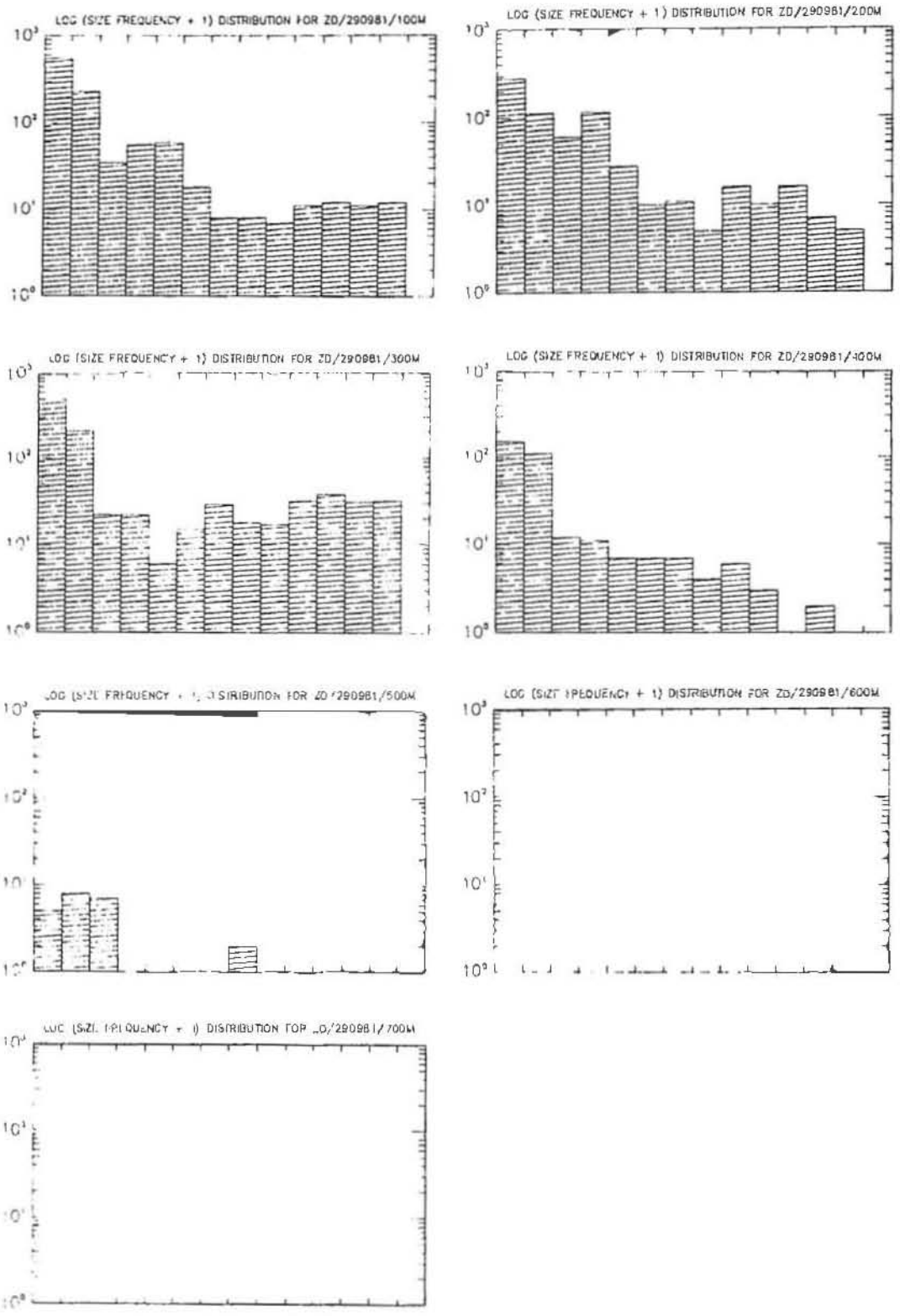


Fig. 3.14 (continued)



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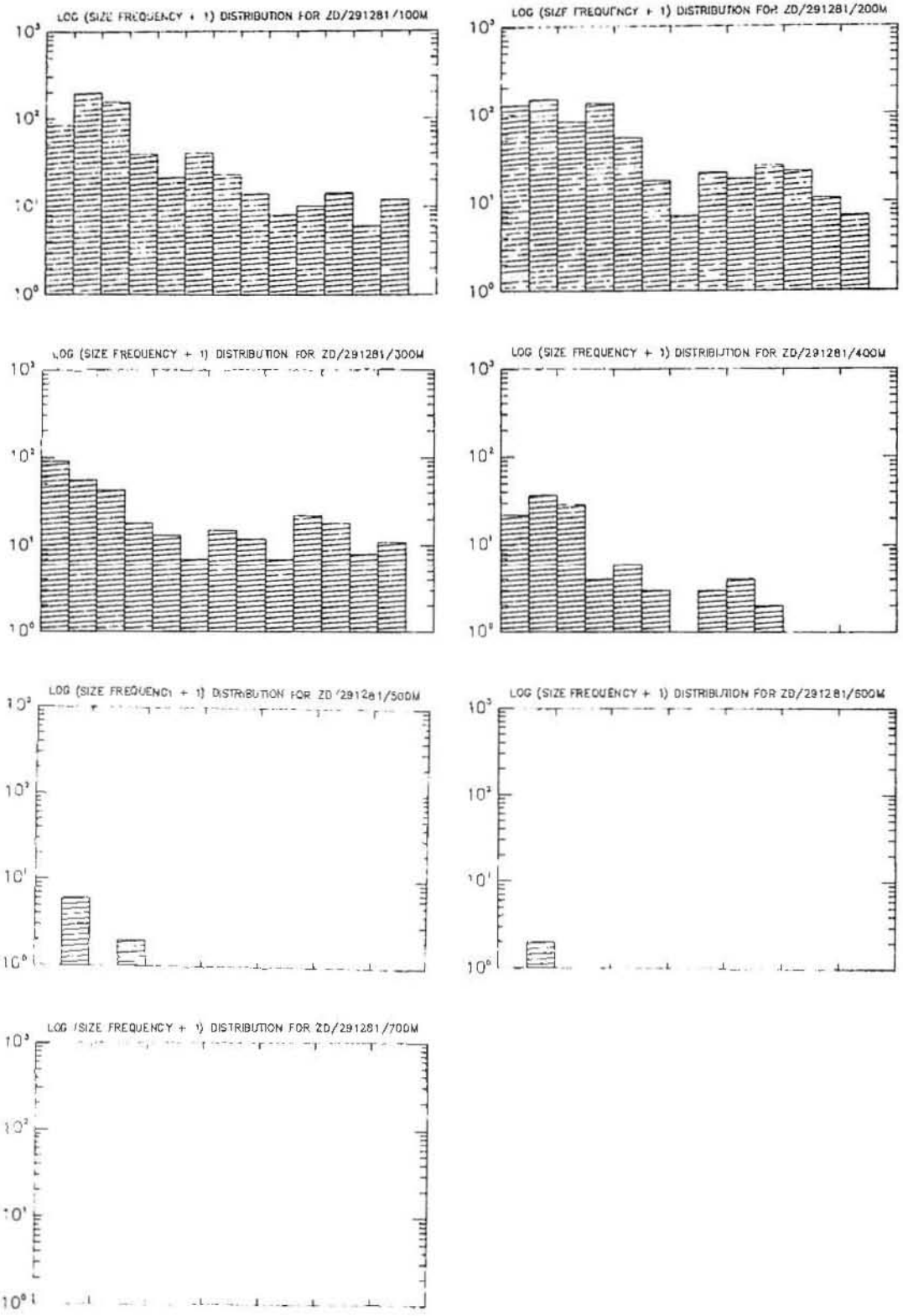

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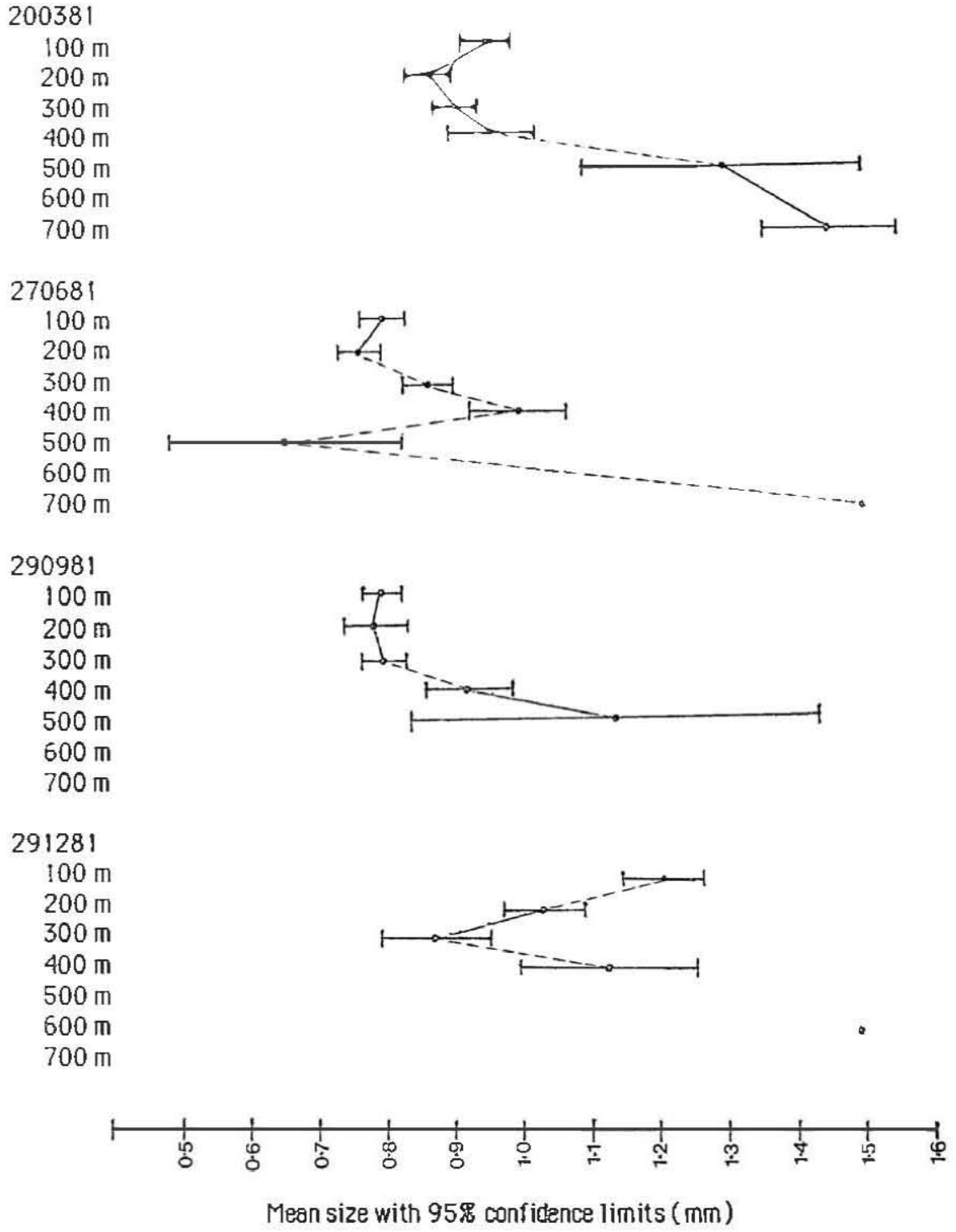


Fig. 3.15 Changes in the mean size of *Zeacumantus* group 1 animals over the transect and through the seasons. Dotted lines indicate significant differences at 5%

suggesting a period of rapid summer growth (although the value of skewness as an indicator could be unreliable with only 2 size classes, inspection shows that is is reasonable for *Zeacumantus* group 1). The skewness and size decrease at 100 m and 200 m by 200381.

The slight increase in size at 300 m from 270681/290981 to 291281/200381 is accompanied by a small decrease in positive skewness. There are similar trends in size and skewness at 400 m on 291281 but the skewness actually becomes negative. *Zeacumantus* group 1 animals, therefore, show a period of rapid summer growth at all distances from 100 m to 400 m.

Changes in the abundance of group 1 animals are closely mirrored by changes in the abundance of 0 mm animals, although both size classes are well represented. The grouping, therefore, appears reasonable. In general, group 1 abundances are fairly constant from 100 m to 300 m before a sharp fall at 400 m. Through most of the year numbers are highest on 200381 and decrease slightly on 270681 and 290981 before a marked reduction on 291281. Relative abundances are high and vary little from 100 m to 500 m and fall sharply at 600 m. An exception is on 291281 when there is a steady increase from a low at 100 m to a high at 600 m. This suggests a greater rate of exit from group 1 high on the beach in summer.

Zeacumantus , then, shows a high autumn recruitment of group 1 animals. These animals grow slowly over winter and spring before a period of rapid summer growth that results in a loss of animals to group 2. The summer growth appears to be most rapid high on the beach.

Group 2 (2 - 4 mm)

In general, there is a trend for a decrease in mean size of group 2 (Fig. 3.16) from high on the beach to low on the beach. There is little change in the mean size with season, except for a decrease at 100 m and a slight decrease at 400 m on 291281. These decreases are accompanied by an increase in positive skewness, indicating an influx of young animals from group 1. At 100 m this positive skewness decreases from 291281 through 200381 to be negligible on 270681 and finally negative on 290981. This suggests a steady growth of animals after the 291281 influx. Changes in skewness throughout the year are less marked at other distances and skewness remains positive. At 200 m, however, skewness on 291281 is almost zero, in contrast to other distances on that date, indicating little entry of young animals to group 2 over summer. In fact, high positive skewness at 200 m on 200381 suggests an autumn influx.

Marked changes in abundance of group 2 animals through the year are found only at

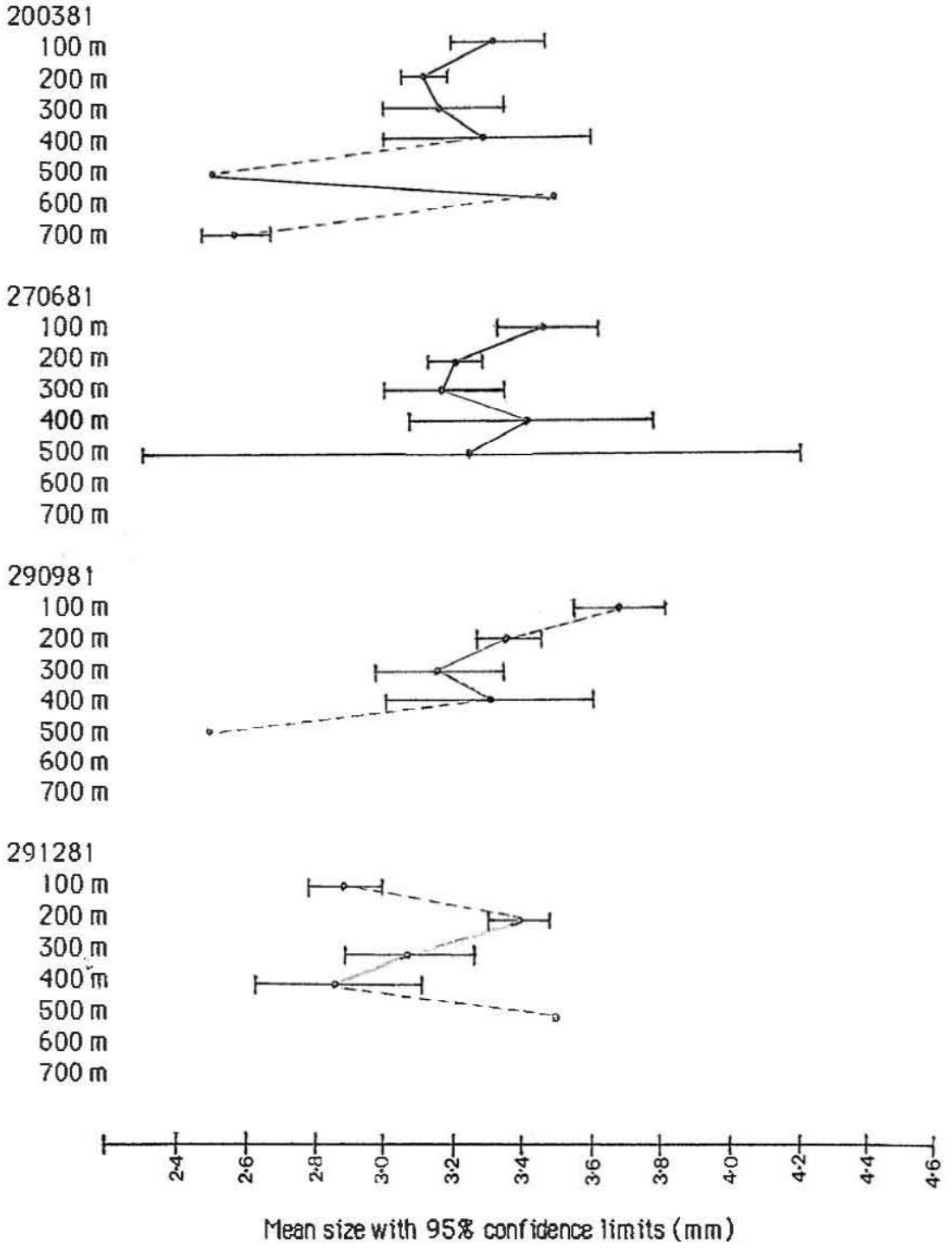


Fig. 3.16 Changes in the mean size of *Zeacumantus* group 2 animals over the transect and through the seasons. Dotted lines indicate significant differences at 5%.

100 m and 200 m. At 100 m, numbers are highest on 291821 with other seasons having lower numbers. At 200 m, numbers are highest on 200381 and decrease through 270681 to 290981 before increasing on 291281.

These changes in the abundance, skewness and mean size of group 2 reflect an influx of young animals to the group over summer (100 m) and autumn (200 m). Those animals then grow steadily over the following winter and spring.

Group 3 (5 - 12+ mm)

Mean size of group 3 (Fig. 3.17) changes little through the year, except at 100 m when there is a slight decrease on 290981 and a significant decrease on 291281. Also, the mean size at 300 m is slightly higher on 200381 than at other times of the year.

Marked departures from zero skewness are only evident at 100 m and 400 m. At 100 m, skewness is negative on 200381 but approaches zero through 270681 to 290981 before becoming positive on 291281. This suggests a gradual influx of young animals over winter and spring, followed by a large summer influx. The abundance of group 3 at 100 m is fairly constant through the year but increases slightly on 291281.

Although there are generally only slight changes in abundance and mean size at 400 m, skewness at this distance is strongly positive on 270681 and decreases to become negative on 291281 before becoming positive again on 200381. Low numbers on 291281 make the skewness figure on that date suspect but it does appear that, at 400 m, 200381 and 270681 are characterised by relative youthfulness of group 3 animals.

Summary

Zeacumantus is represented by 0 mm animals throughout the year, but autumn is associated with major recruitment. Those animals grow slowly over winter and spring prior to a period of rapid summer growth, particularly high on the beach. Year 0+ animals are represented by group 1 animals while group 2 and group 3 probably represent year 1+ and 2+ respectively.

3.3.7 *Salinator*

The size frequency distribution of (Fig. 3.18) was divided into two groups:

Group 1 (0 - 1 mm)

Group 1 animals are relatively uncommon in autumn and winter making comparisons of mean sizes difficult. There are, however, significant increases in mean size (Fig. 3.19) from 290981 to 291281. These occur at all distances except 200 m, where the increase is slight, and 300 m where there is a decrease. At all distances except 200 m and 300 m these increases are accompanied by decreases in positive skewness, particularly at 100 m, where the skewness becomes negative. At 200 m and 300 m there is an

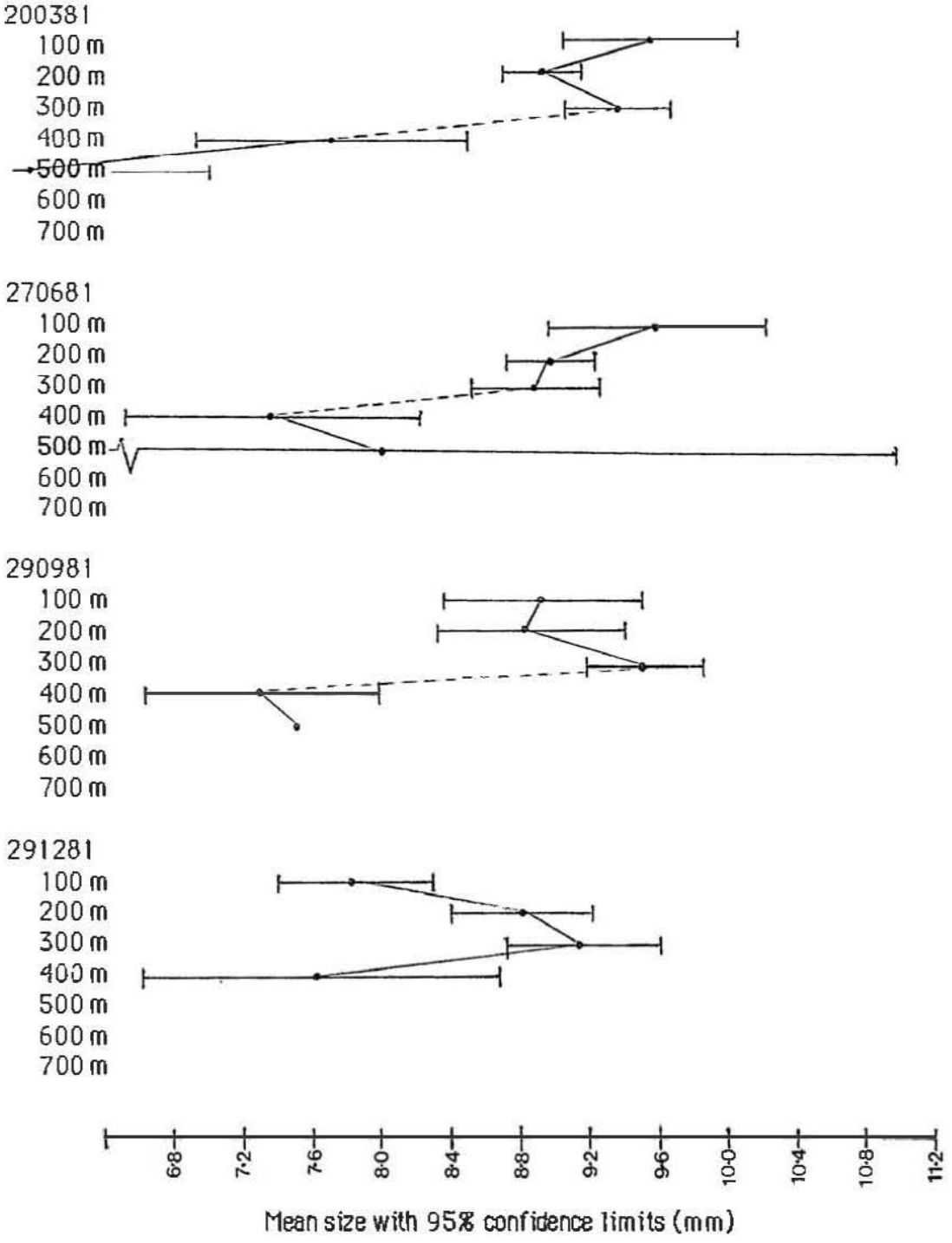


Fig. 3.17 Changes in the mean size of *Zeacumantus* group 3 animals over the transect and through the seasons. Dotted lines indicate significant differences at 5%.

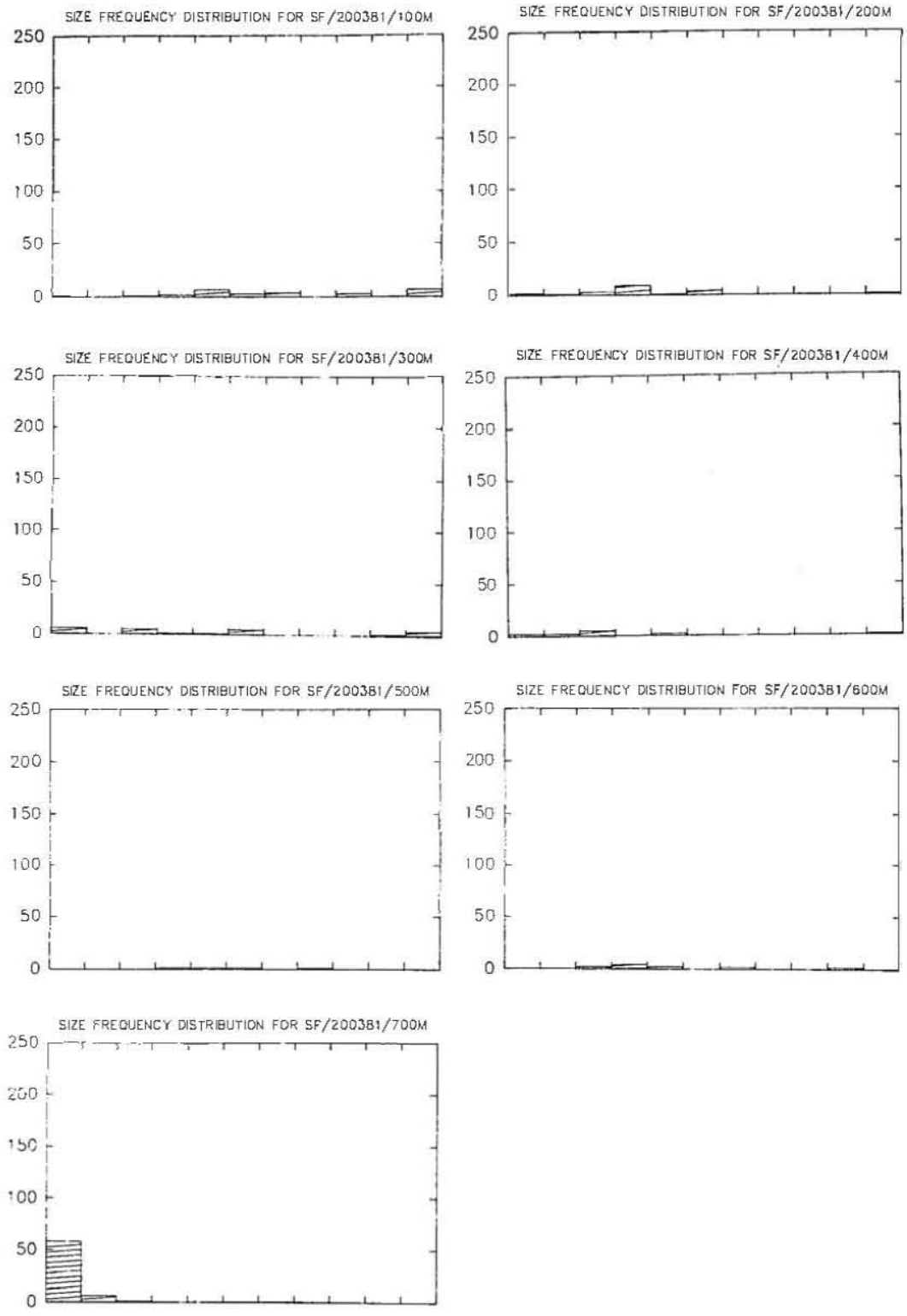


Fig. 3. 18 Size frequency distributions of *Salinator* at dispersion transect stations. Size class axes range from 0 mm to 10+ mm in 1 mm intervals.

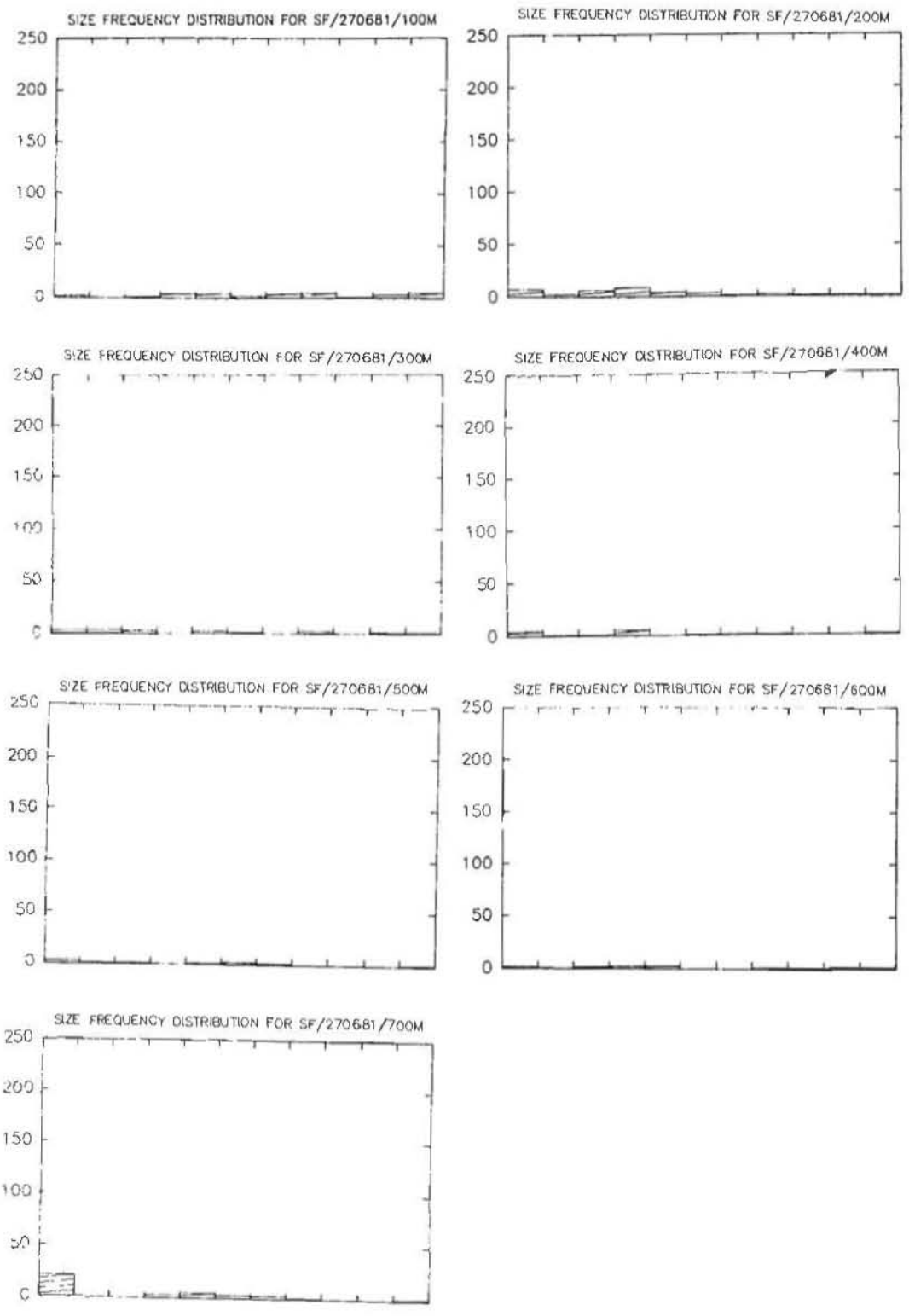


Fig. 3.18 (continued)

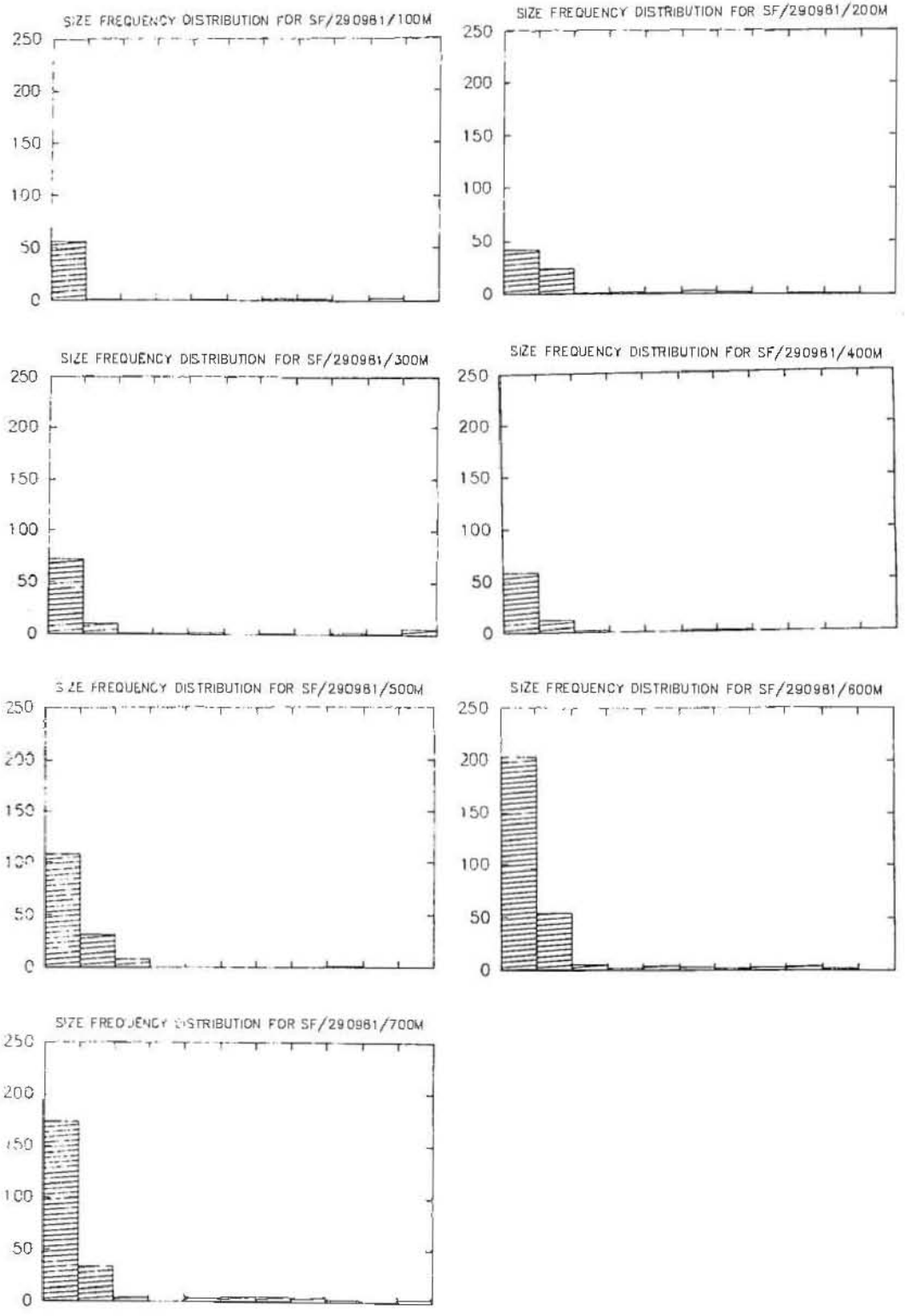


Fig. 3.18 (continued)

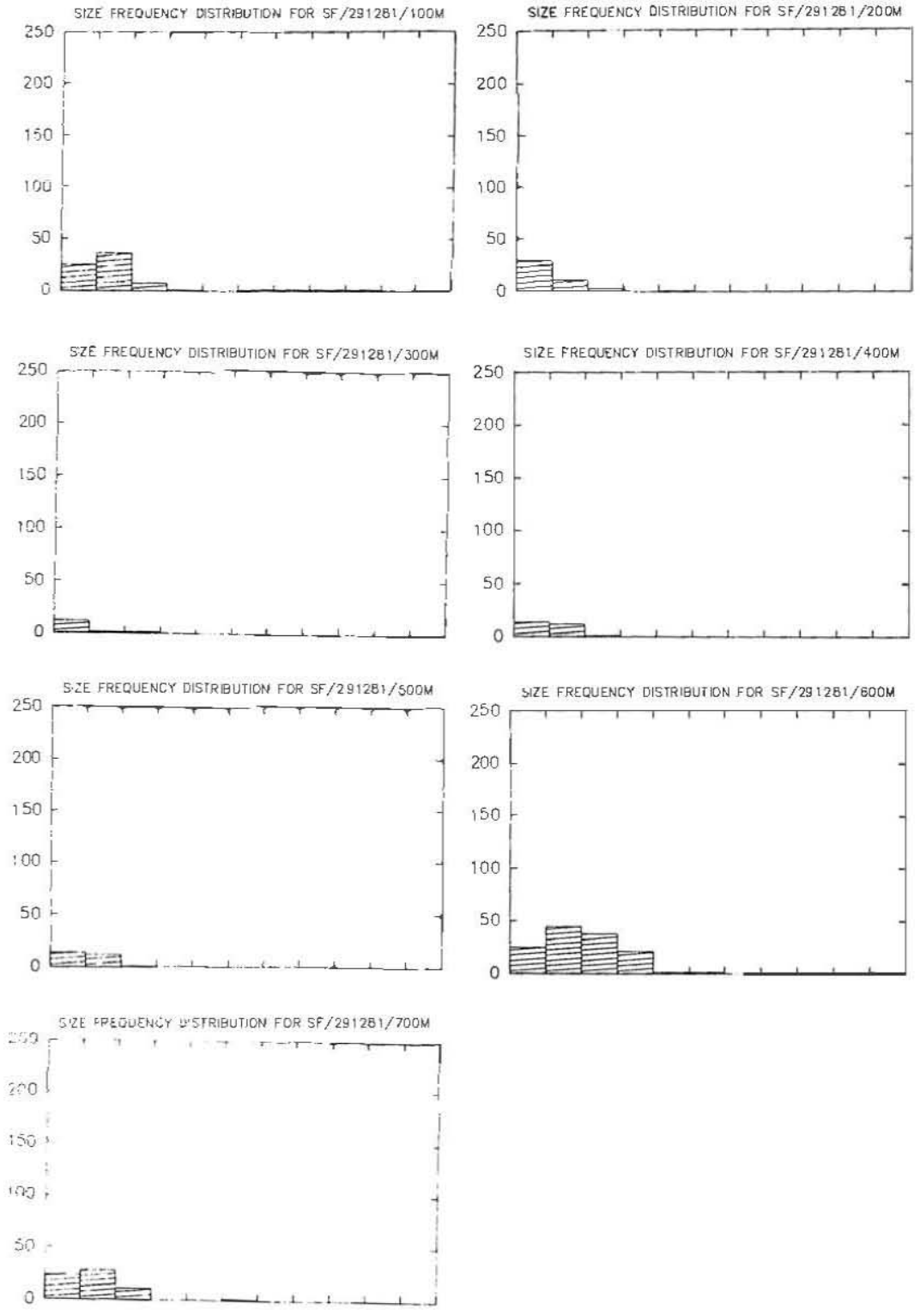


Fig. 3.18 (continued)

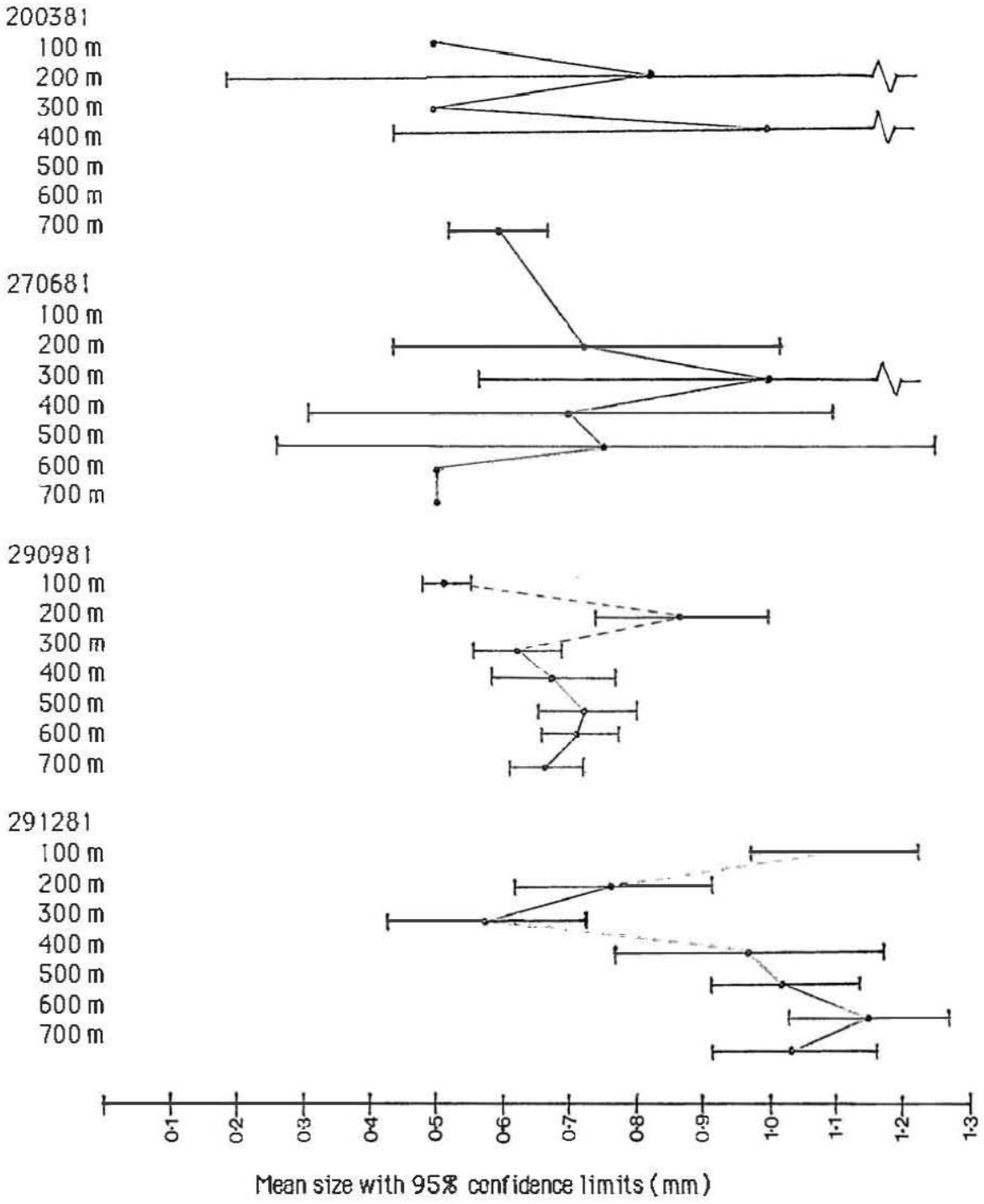


Fig. 3.19 Changes in the mean size of *Salinator* group I animals over the transect and through the seasons. Dotted lines indicate significant differences at 5%

increase in positive skewness from 290981 to 291281.

Throughout the year there is a general increase in group 1 abundance from 100 m to 700 m, particularly low on the beach. Group 1 animals are uncommon on 200381 and 270681, except at 700 m. There is a pronounced increase in numbers over the whole beach on 290981. Numbers then drop on 291281, except at 100 m.

Salinator appears to have a period of spring recruitment, as reflected by the low mean size, high positive skewness and high abundance of group 1 on 290981. There is a then a period of spring/summer growth with significant increases in mean size at most distances. At 100 m the increase is particularly marked due to the relatively low mean size at that distance on 290981. The comparative changes in size and skewness at 100 m between 290981 and 291281, together with the maintainance of high group 1 numbers there, suggest a slower growth of young animals.

Group 2 (2 - 10+ mm)

There is little change in the mean size of group 2 (Fig. 3.20) during the year, except on 291281 when there are significant decreases at 100 m, 600 m and 700 m and slight decreases at other stations. Skewness at stations high on the beach (100 m - 400 m) shows a general decline from high positive on 200381 to low positive, or negative, on 290981. On 291281 abundances are low in this region. Lower on the beach (500 m - 700 m), a similar decline occurs before a sharp increase to high positive skewness on 291281.

Above 400 m, abundances are lowest on 290981 and 291281 and highest on 200381 and 270681. The reverse is true below 400 m.

The above changes reflect the different growth rates of high beach and low beach group 1 animals following the spring recruitment.

3.3.8 *Bembicium*

Bembicium is common only in the top 50 m of the beach and becomes rare below 100 m. This resulted in few animals being included in the dispersion samples (Fig. 3.21).

From the small number sampled, it appears that *Bembicium* recruitment occurs over the summer/spring period. Only on 291281 are 0 mm animals present. On 200381 there is an increase in abundance, a slight decrease in mean size (Fig. 3.22) and a strong positive skewness at 100 m (the size frequency distribution was treated as a single group). Numbers are also greater at 200 m and 300 m on this date. There are subsequent small increases in mean size through 270681 to 290981 before a decrease on 291281. These observations are supported by the frequency data obtained from the

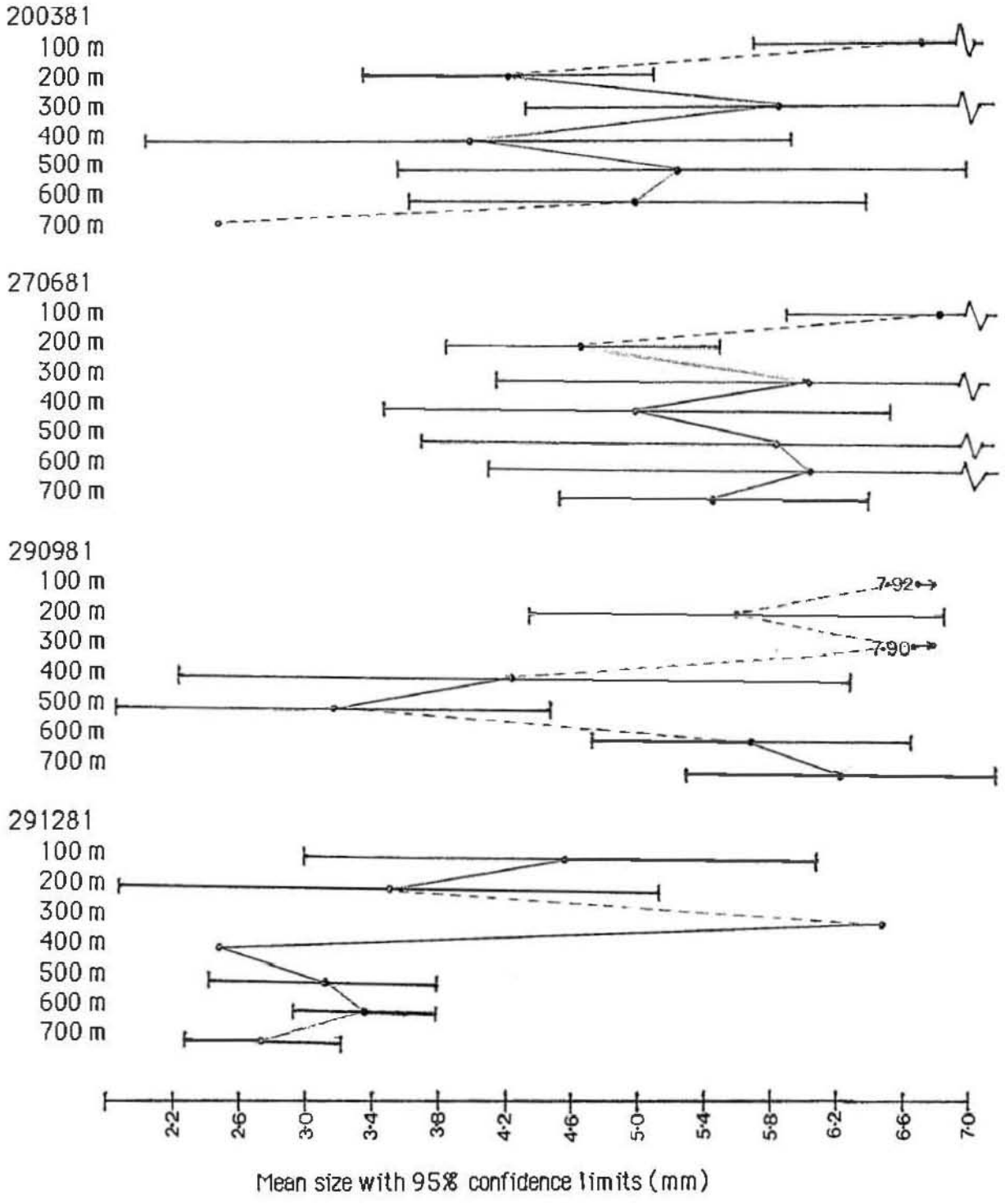


Fig. 3.20 Changes in the mean size of *Salinator* group 2 animals over the transect and through the seasons. Dotted lines indicate significant differences at 5%

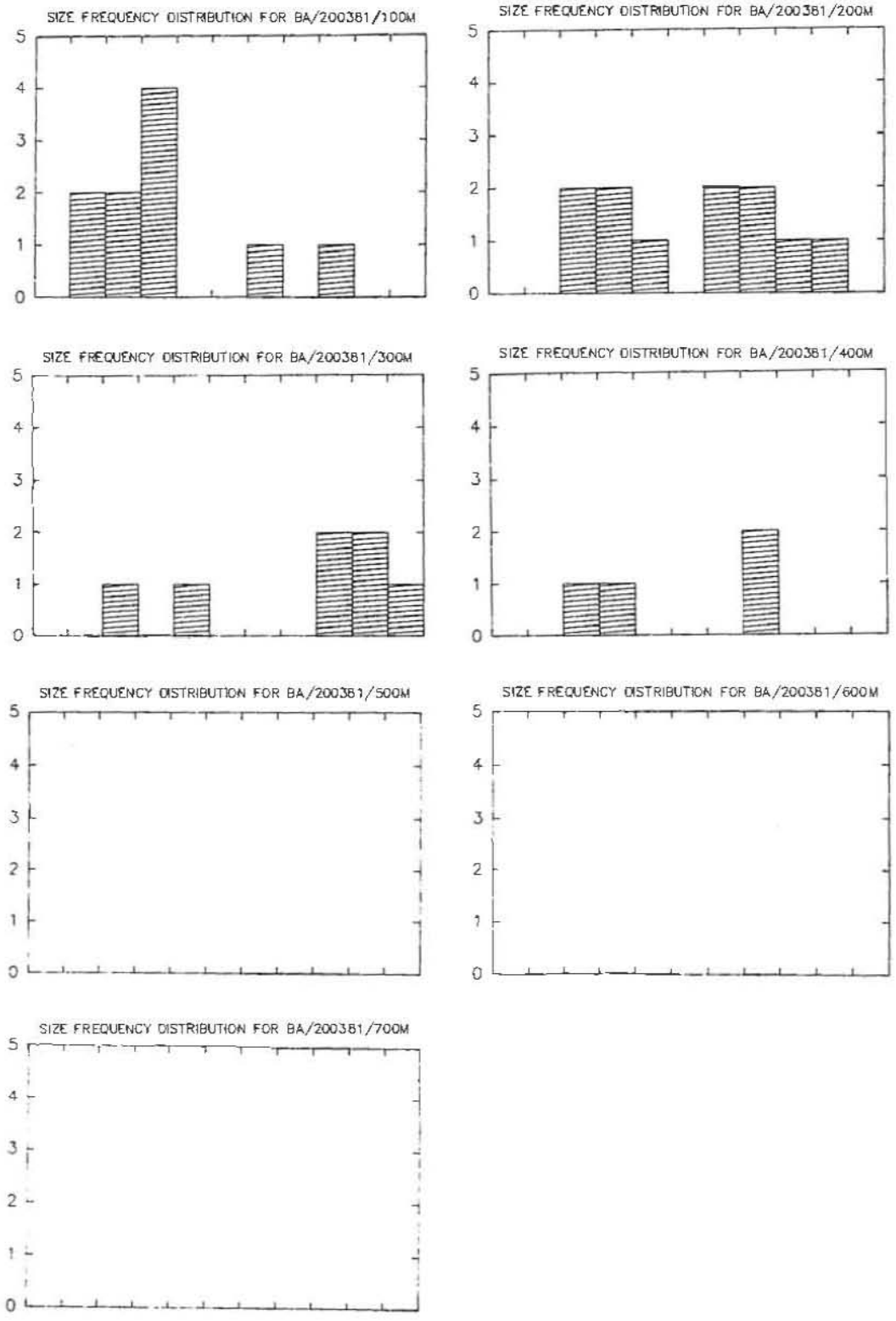


Fig. 3.21 Size frequency distributions of *Bembicium* at dispersion transect stations. Size class axes range from 0 mm to 10+ mm in 1 mm intervals.

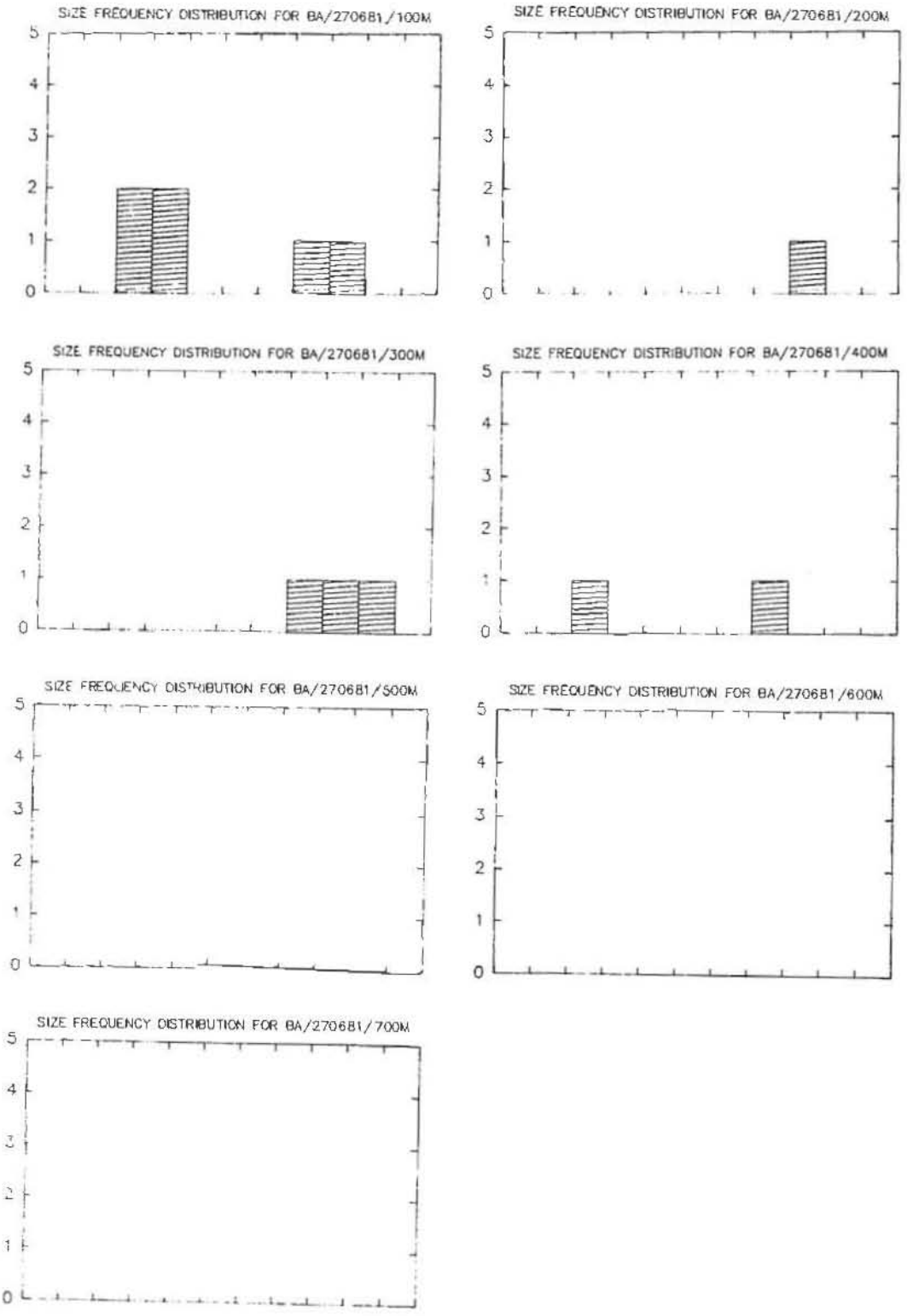


Fig. 3.21 (continued)

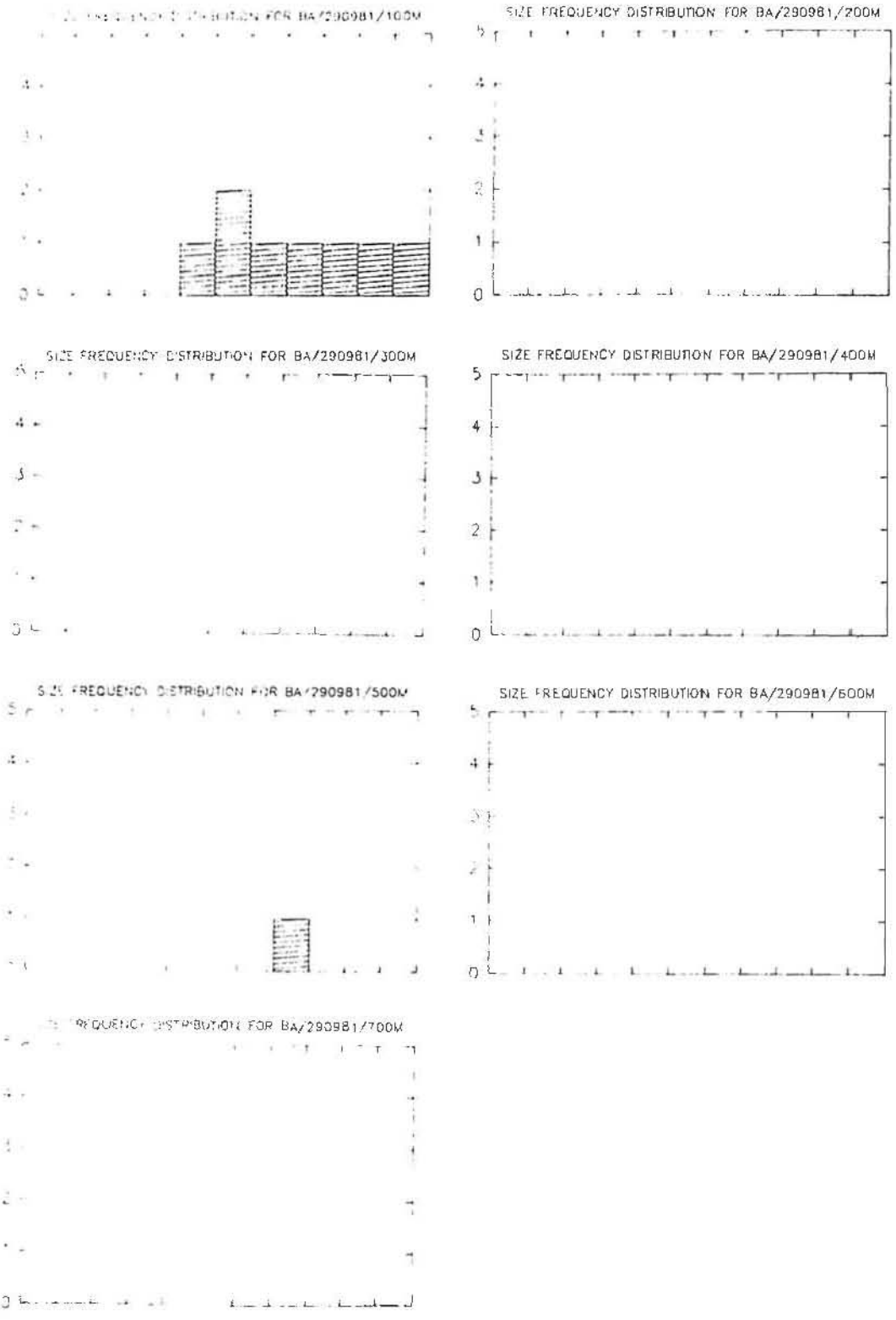


Fig. 3.21 (continued)

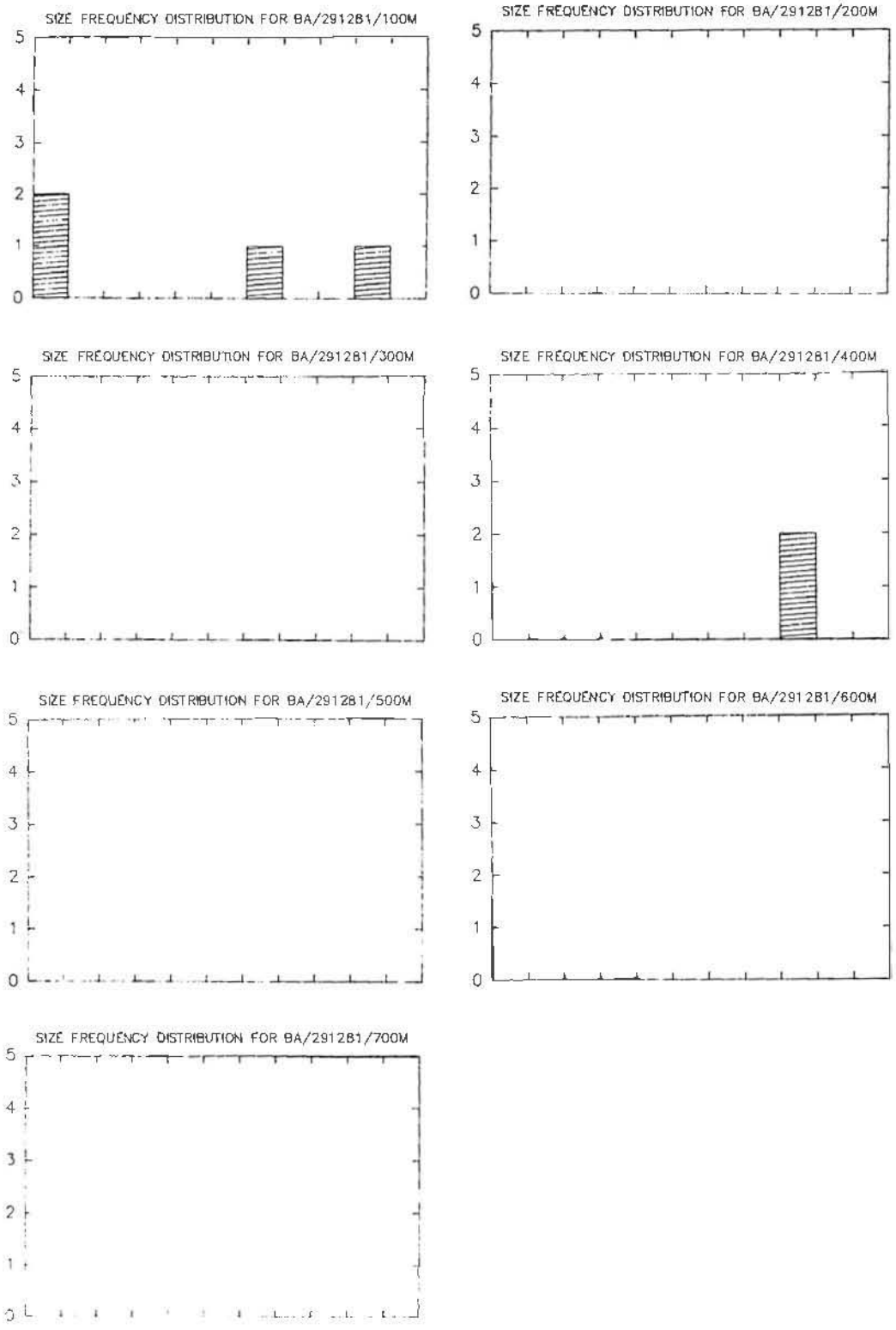


Fig. 3.21 (continued)

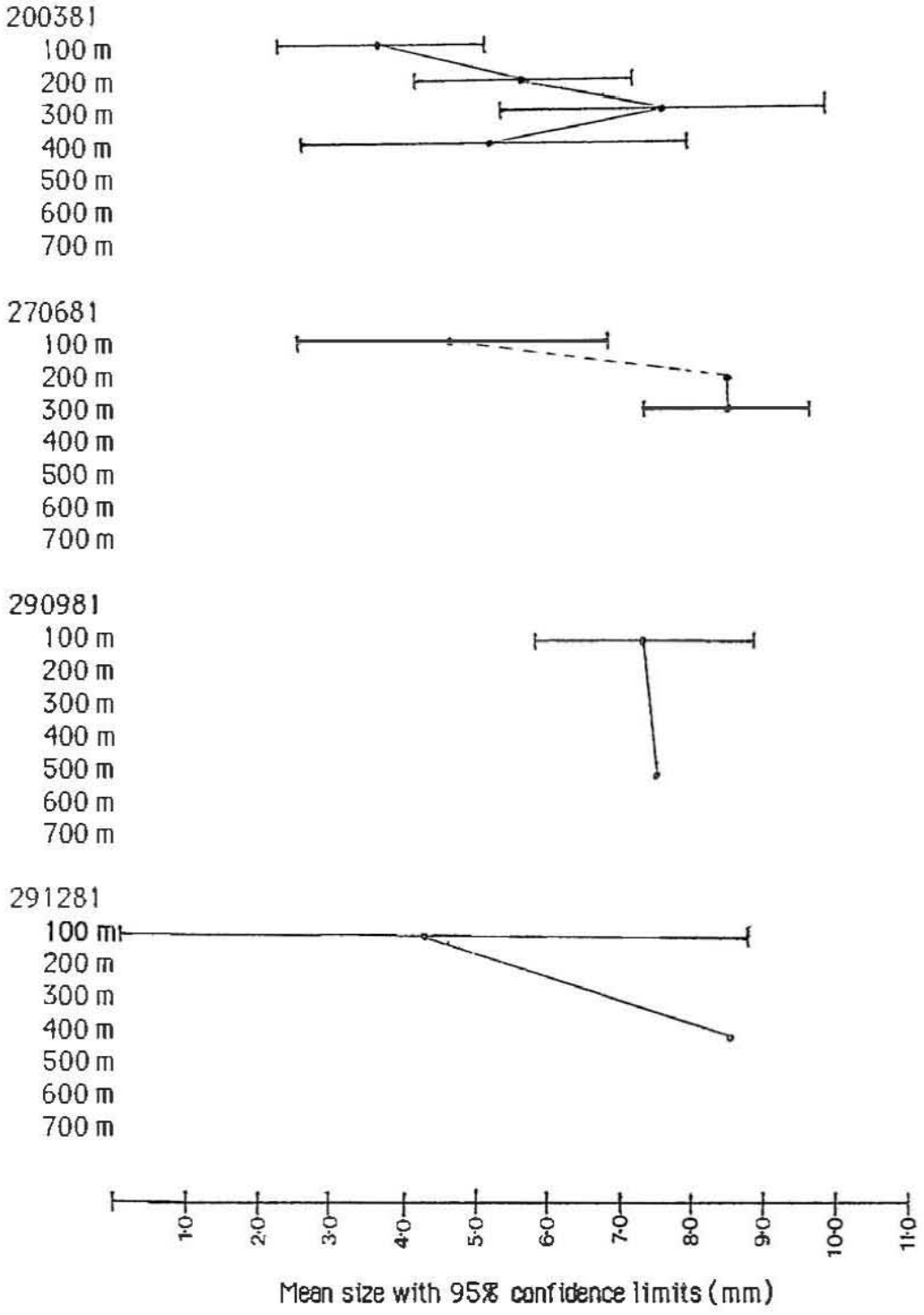


Fig. 3.22 Changes in the mean size of *Bembicium* over the transect and through the seasons. Dotted lines indicate significant differences at 5%

distribution transects.

Bembicium shows summer/autumn recruitment high up on the beach. This is followed by a period of slow, steady growth over winter and spring.

3.3.9 *Notoacmea*

Too few animals were found to allow speculation about seasons of recruitment.

3.3.10 *Rissopsis*

The size frequency distribution (Fig. 3.23) was treated as a single group.

The mean size (Fig. 3.24) varies markedly from the the overall mean only at 200 m, 600 m and 700 m. At 200 m, the mean size is low on 200381, increases significantly on 270681, and remains high on 290981 before dropping on 291281. The increase is accompanied by a movement from positive to negative skewness and the subsequent decrease by a return to posititve skewness.

Rissopsis is rare at 700 m on 291281 and 200381 but on 270681 it becomes more numerous and those animals show an above average size, which increases further on 290981. Similar changes occur at 600 m but there the 270681 size is less. The 600 m increase is associated with a shift from positive to negative skewness, but at 700 m there is a decrease in negative skewness

The patterns of abundance in the various size classes suggest that the period of major recruitment may have fallen between the sample dates. On 200381 and 270681 the high abundances of 0 mm animals supports with the mean sizes and skewness in suggesting an autumn/winter recruitment at 200 m. There appears to be 0 mm recruitment at 100 m over winter/spring although there is no significant decrease in mean size due to the concomitant increase in 1 mm numbers.

At 600 m there is a predominance of 0 mm animals on 270681. These grow to enter the 1 mm class in spring. The abundances, mean sizes and skewness at 700 m suggest a winter recruitment there that continues through to spring.

Thus, recruitment of *Rissopsis* appears to begin in autumn at 200 m and winter numbers are highest there. At 100 m, 600 m and 700 m recruitment begins a season later and is spread over winter and spring. Overall numbers decline in summer.

3.3.11 *Agatha*

The size frequency distribution (Fig. 3.25) of *Agatha* was treated as a single group.

There is no significant change in mean size (Fig. 3.26) through the year. Only on 270681, and then in very low numbers, were 0 mm animals found. Despite this, there are sharp increases in abundances from summer to autumn; it is likely that the recruitment period was missed by the sampling.

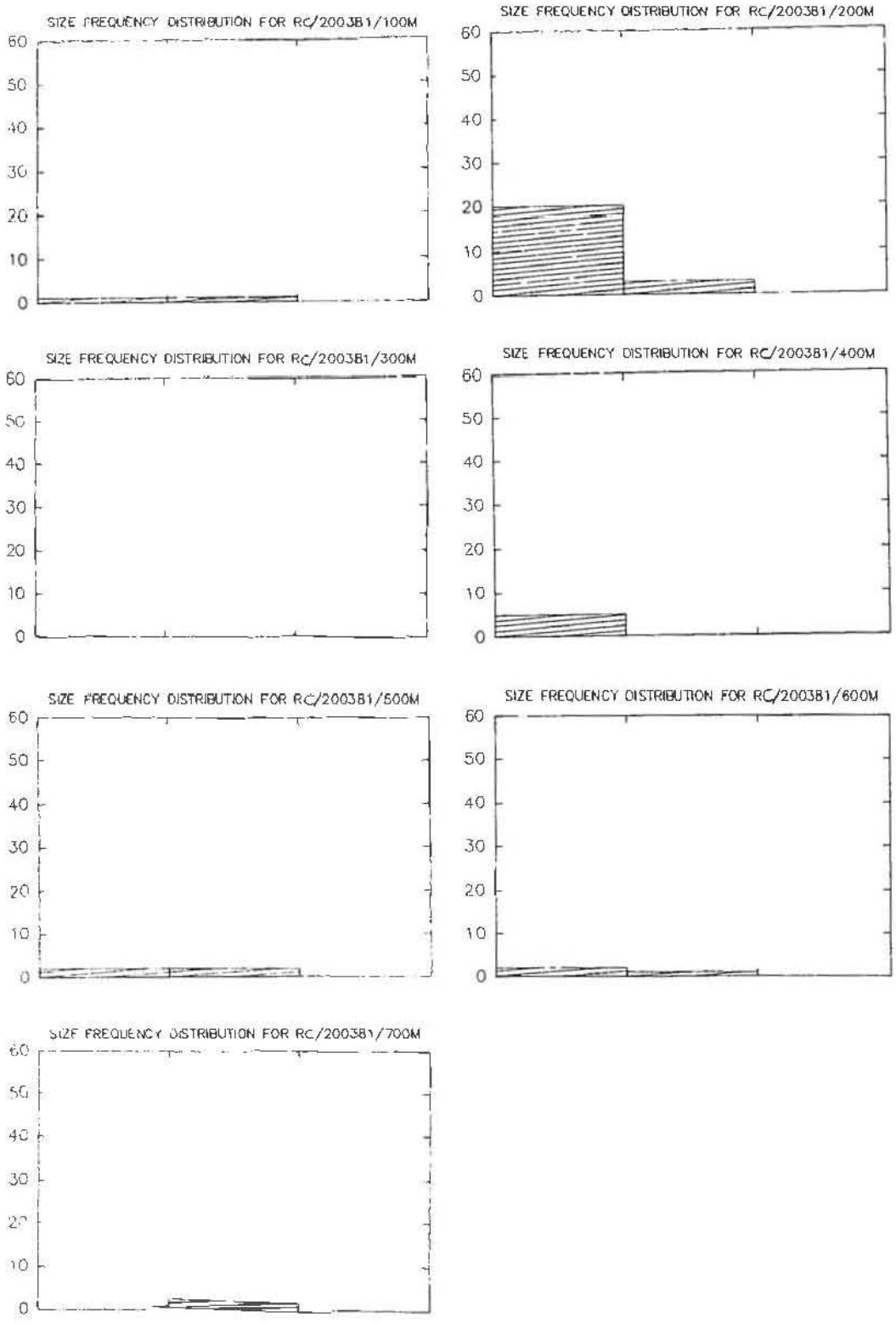


Fig. 3.23 Size frequency distributions of *Rissoposis* at dispersion transect stations. Size class axes range from 0 mm to 2+ mm in 1 mm intervals.

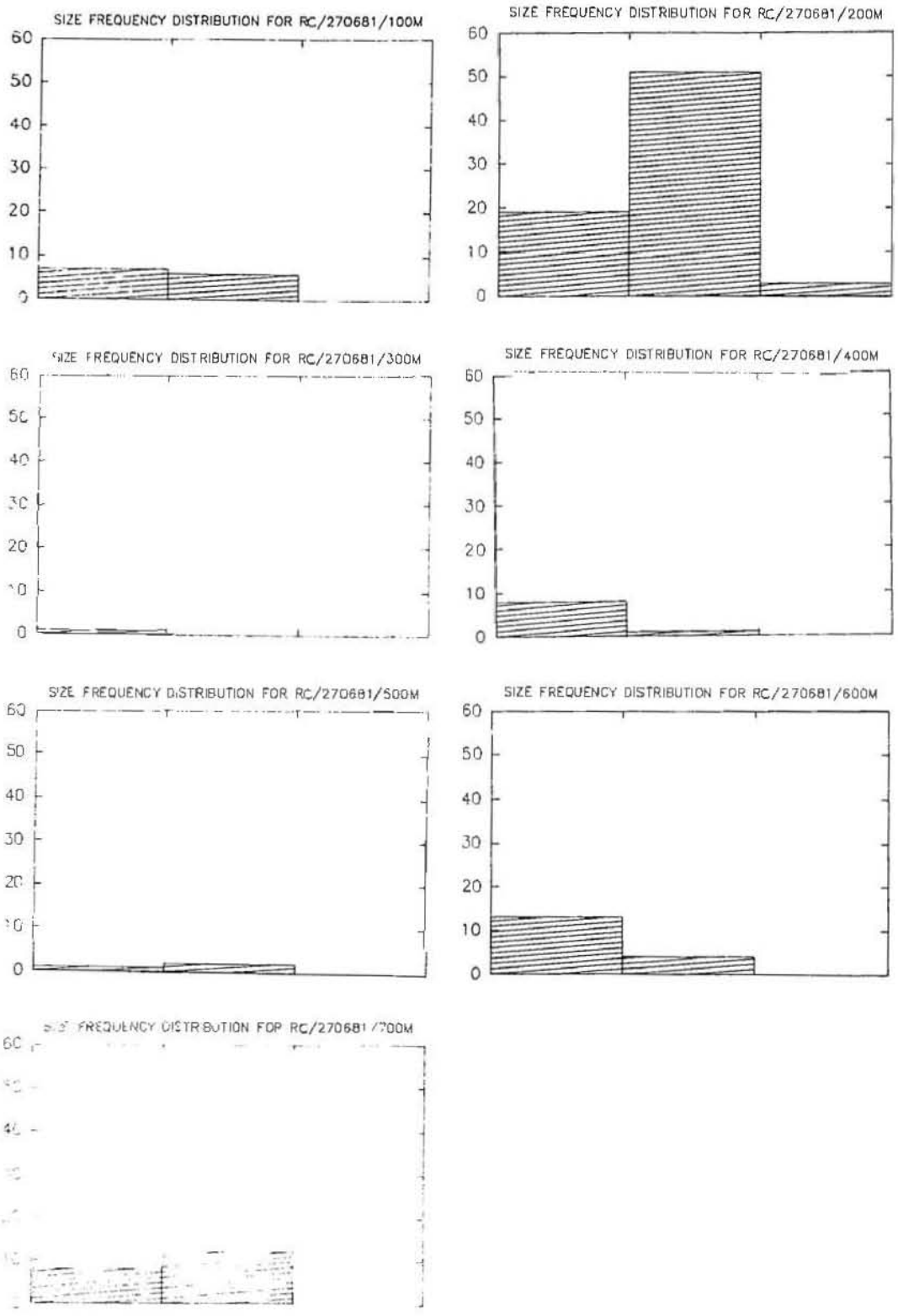
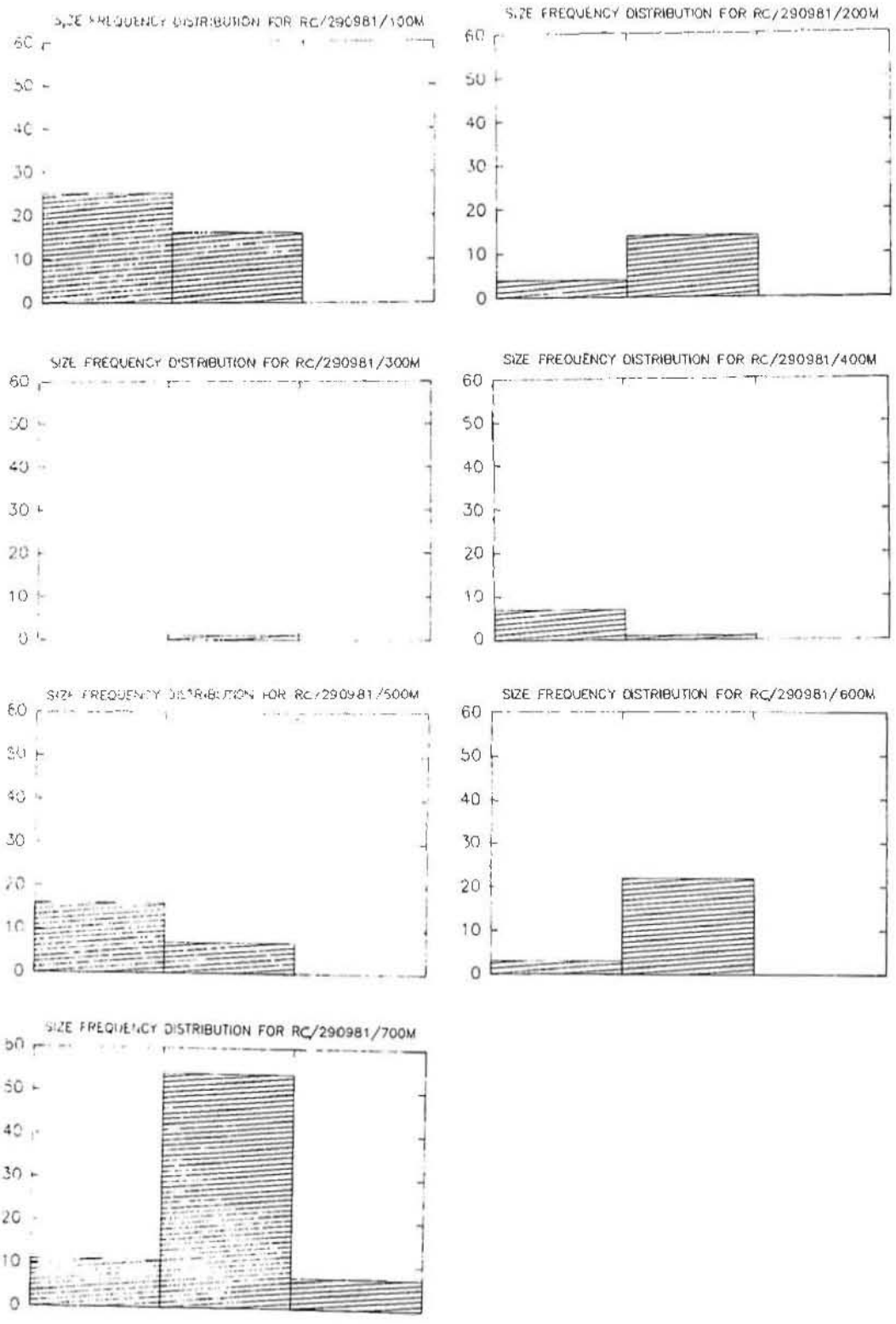


Fig. 3.23 (continued)



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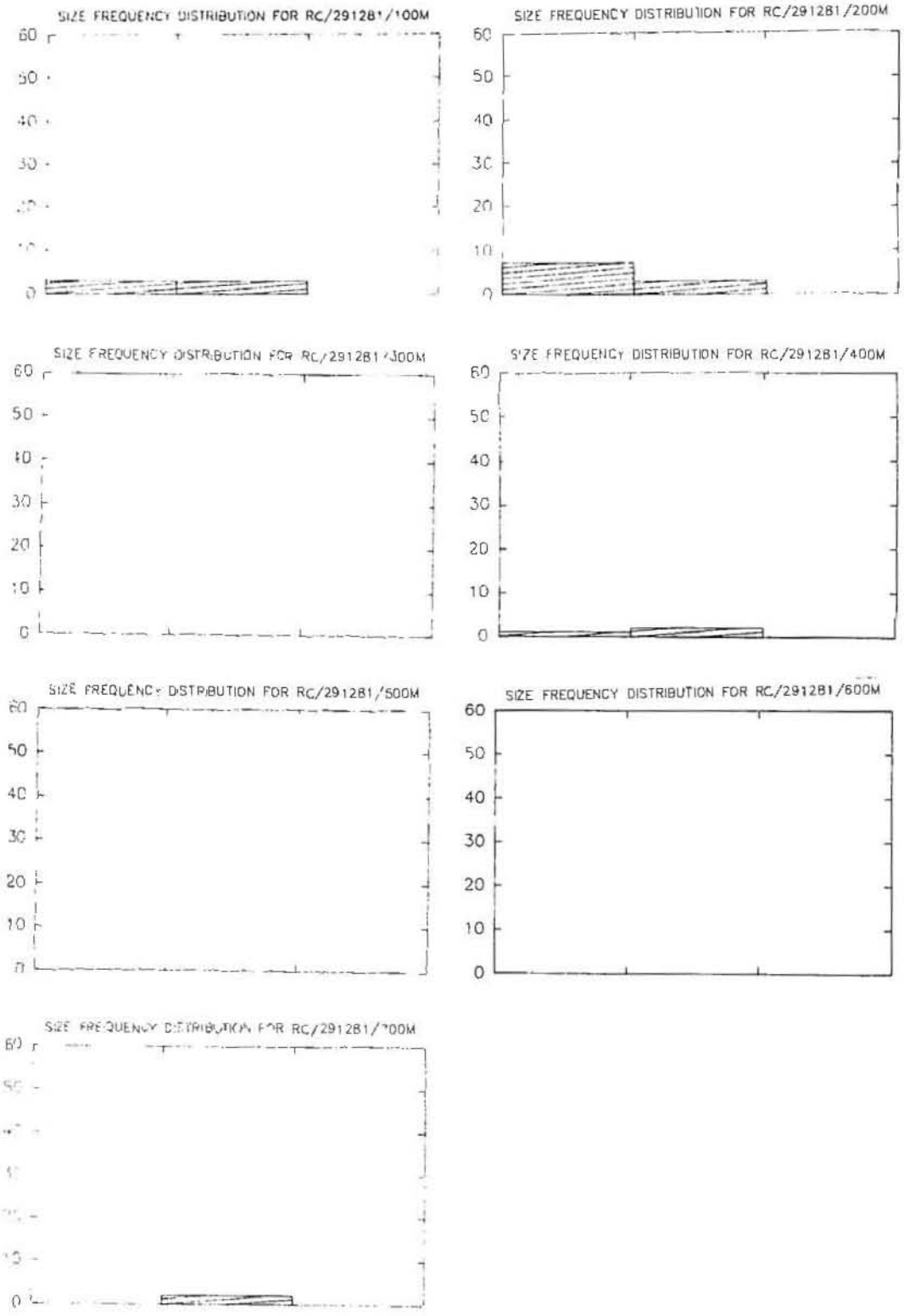

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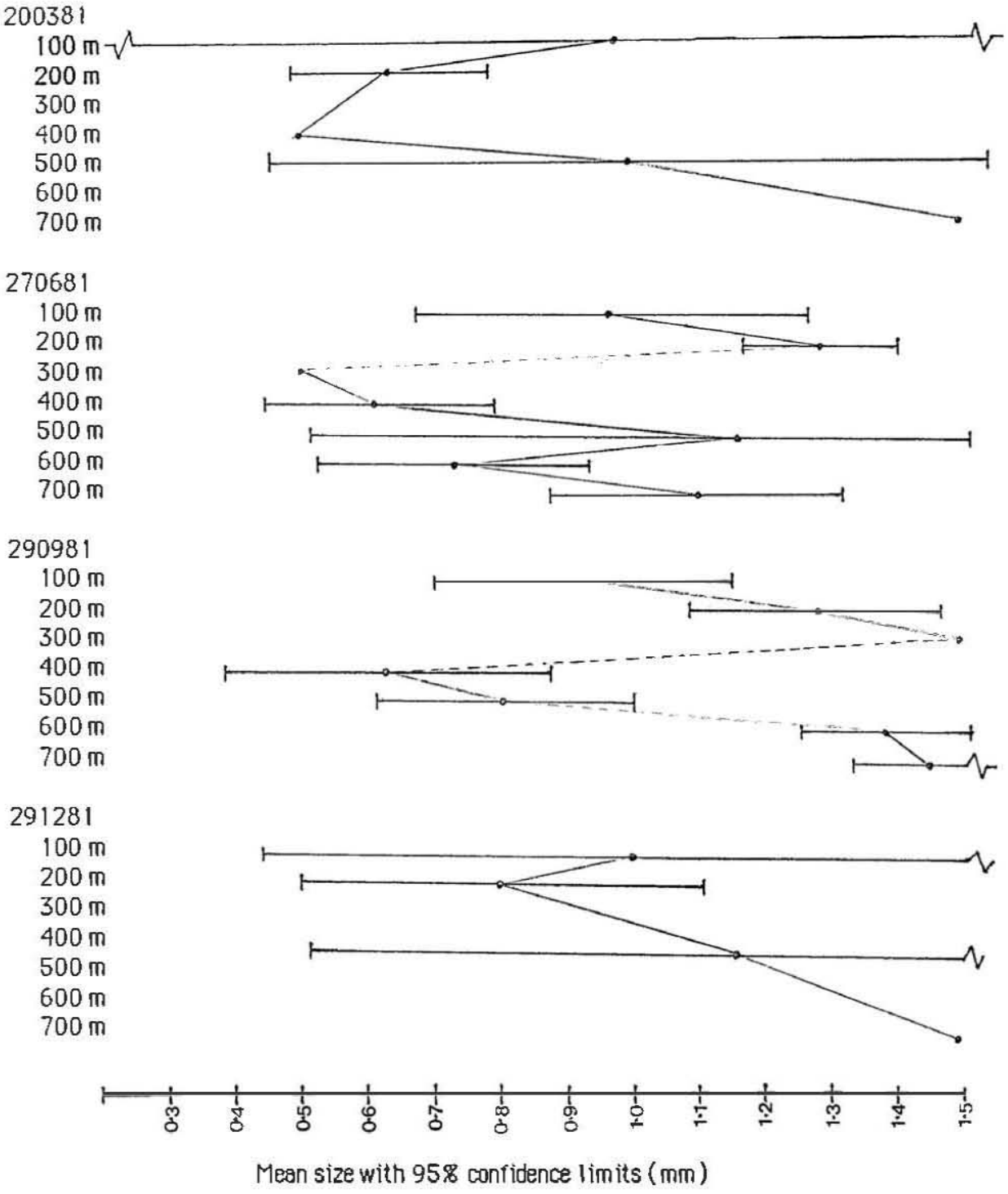


Fig. 3.24 Changes in the mean size of *Rissopsis* over the transect and through the seasons. Dotted lines indicate significant differences at 5%.

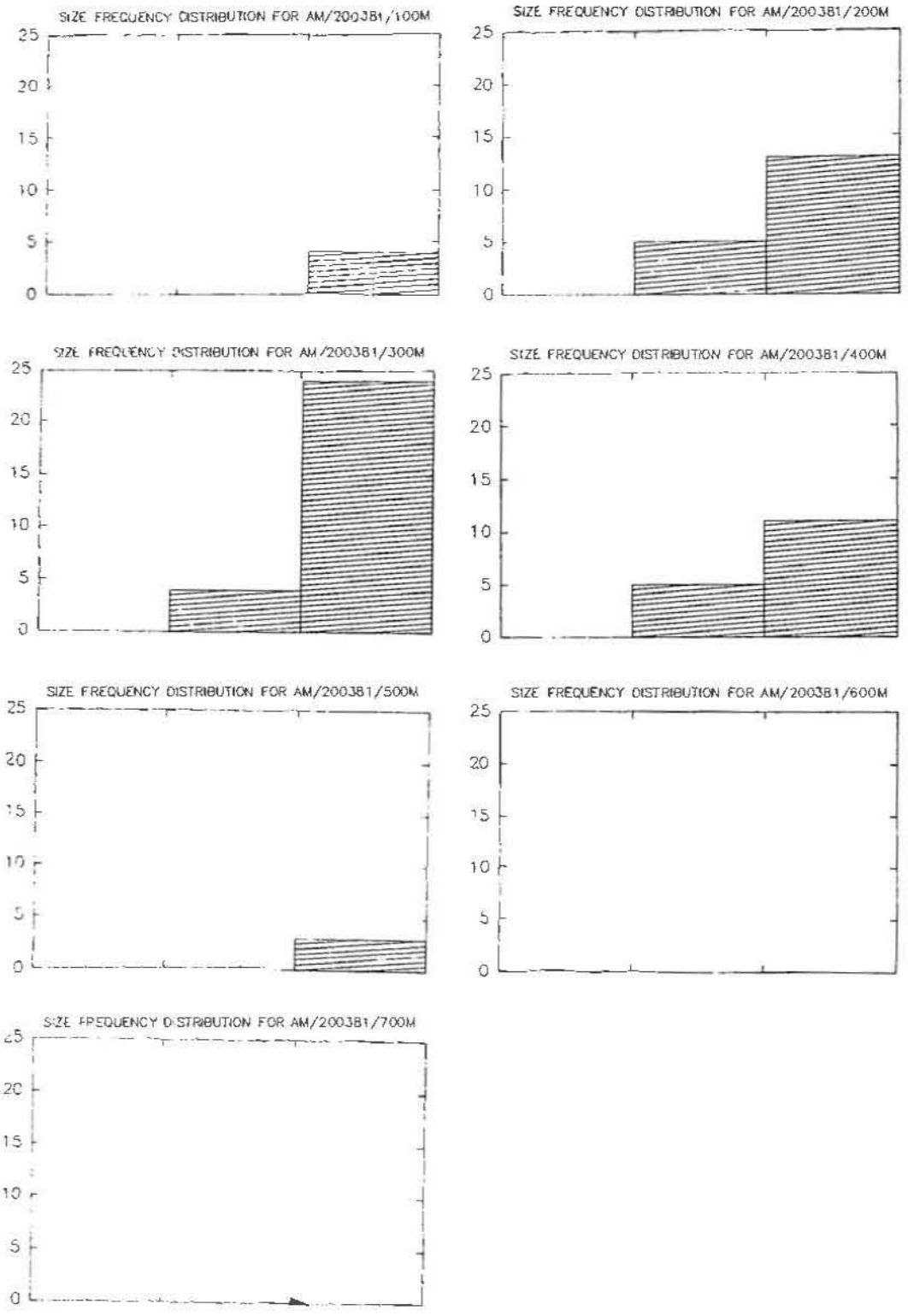


Fig. 3.25 Size frequency distributions of *Agatha* at dispersion transect stations. Size class axes range from 0 mm to 2+ mm in 1 mm intervals.

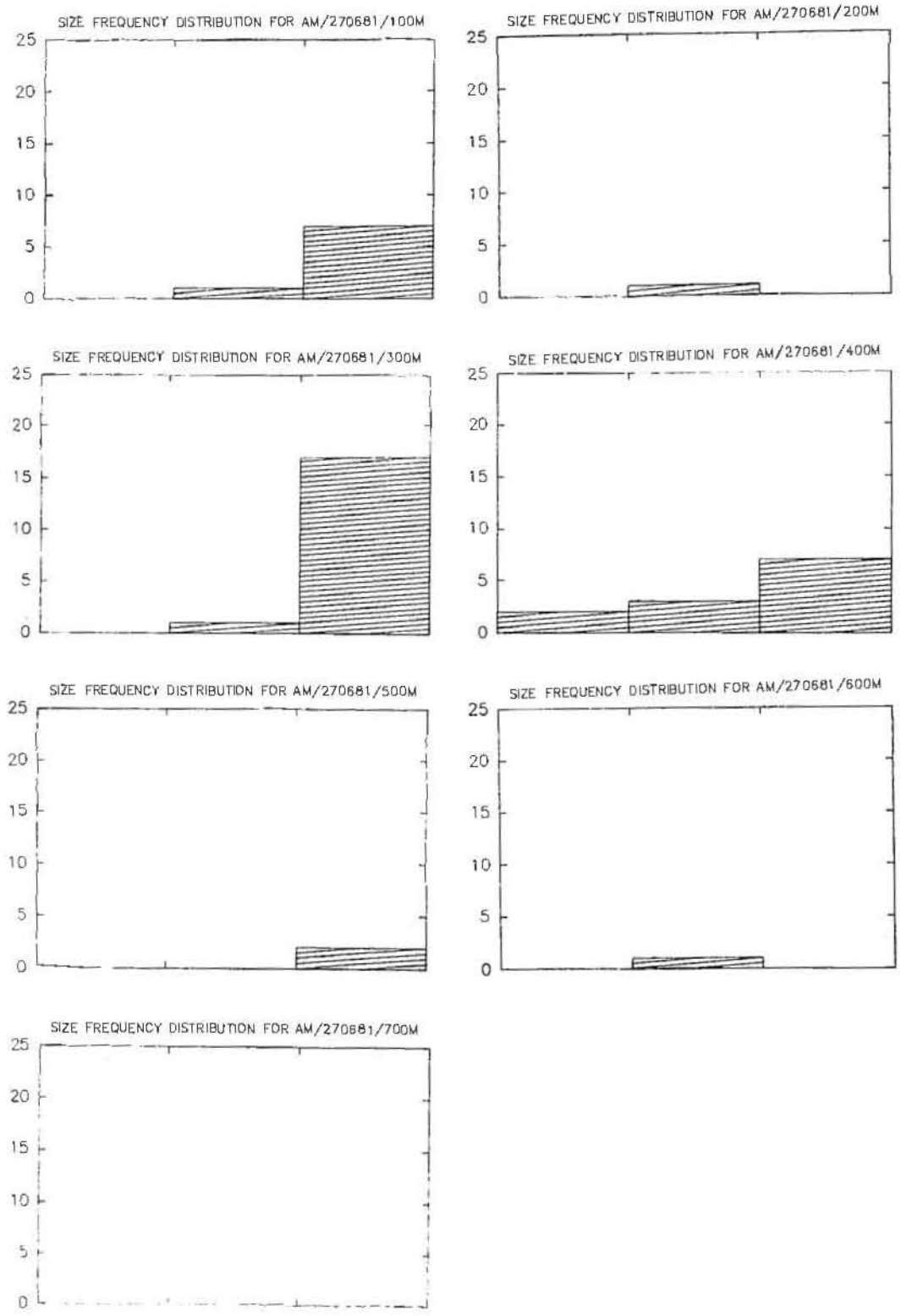
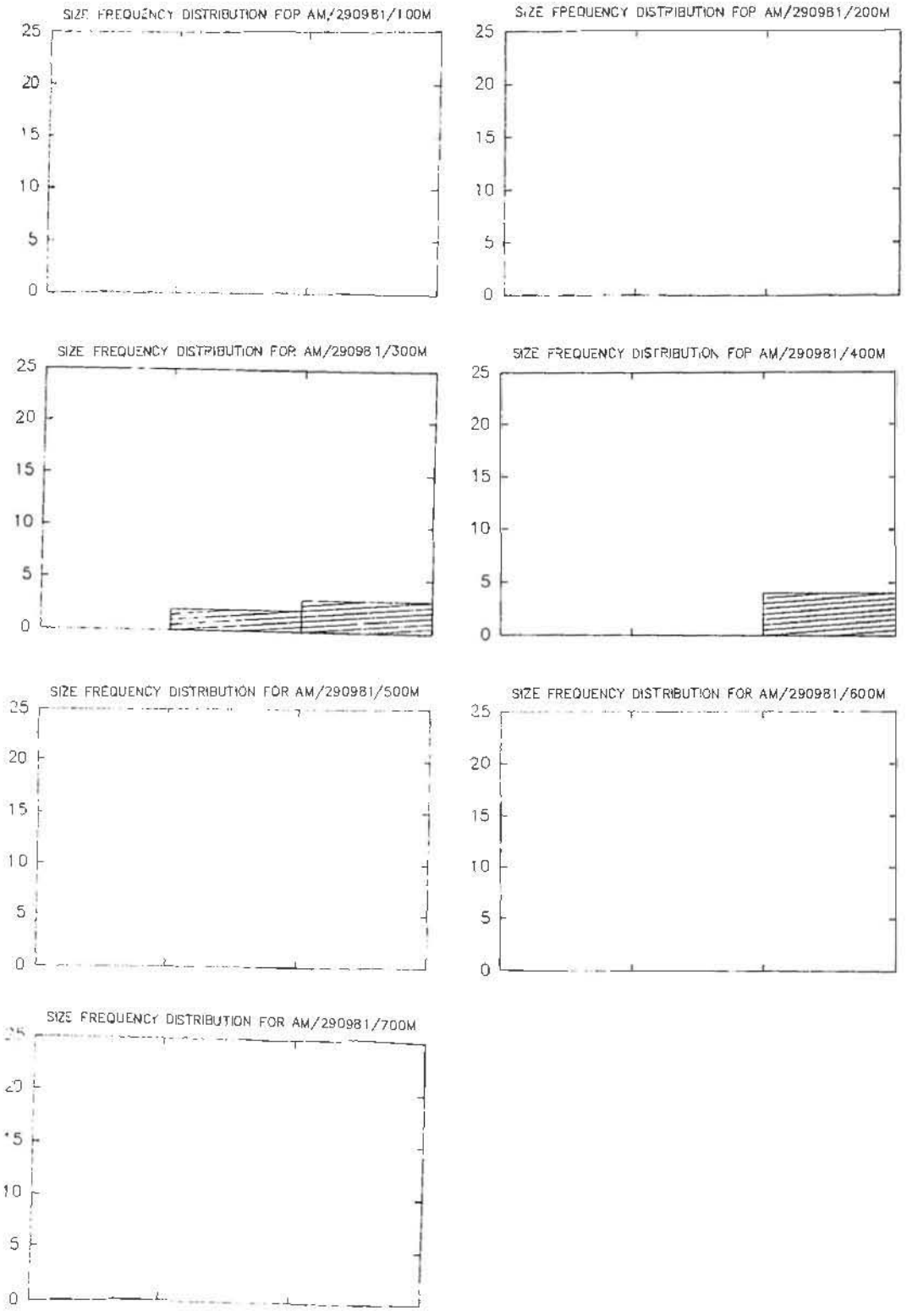


Fig. 3.25 (continued)



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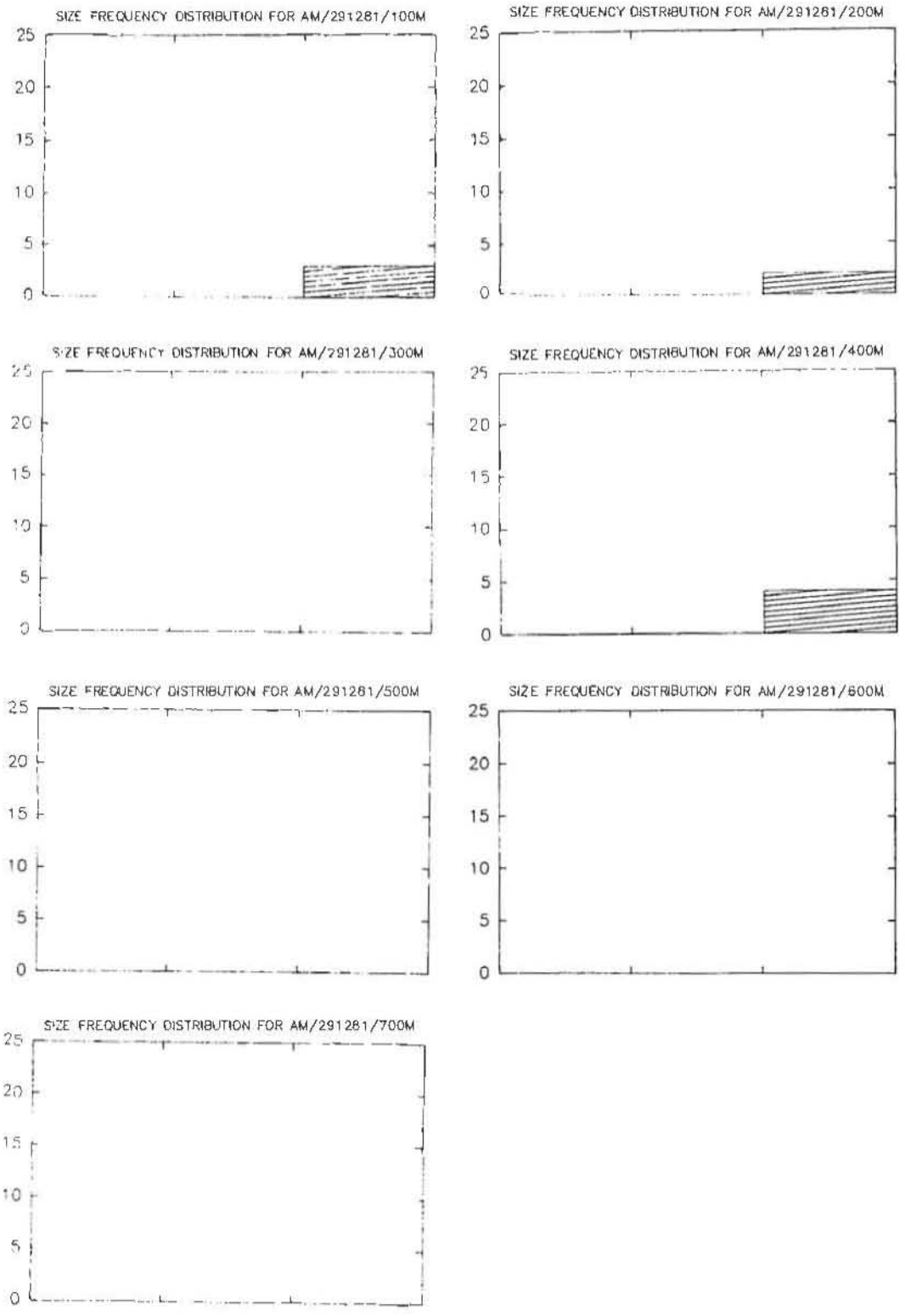


Fig. 3.25 (continued)

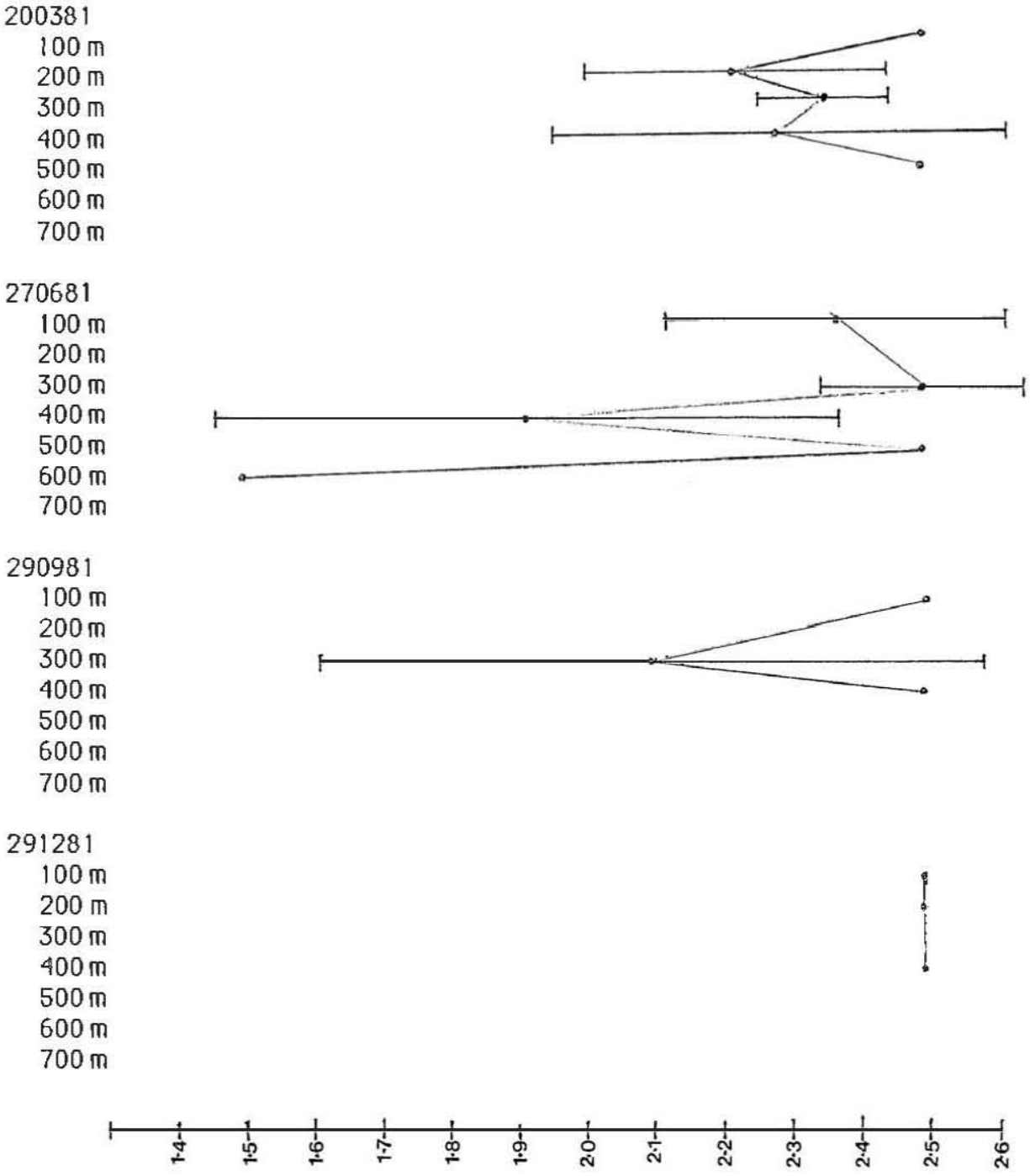


Fig. 3.26 Changes in the mean size of *Agatha* over the transect and through the seasons.

Overall abundance is greatest in autumn and declines over winter and spring to be low in summer; 300 m and 400 m are the areas of greatest abundance. The decrease in numbers from autumn to winter is accompanied by an increase in negative skewness and a (non-significant) increase in size.

Agatha appears to have a late summer/early autumn recruitment. Those animals then grow over winter and spring while overall numbers decline.

3.3.12 *Cylichnina*

The size frequency distribution (Fig. 3.27) was treated as a single group.

Cylichnina shows a clear pattern of recruitment and growth over the year. At all distances the mean size (Fig. 3.28) on 291281 is significantly lower than at any other time of the year. The mean sizes then increase through 200381 to a 270681 maximum. Mean sizes remain high on 290981 but the variability becomes greater with a decrease in overall abundance.

The low mean sizes on 291281 are associated with high positive skewness which decreases over autumn and spring to be close to zero, or negative, on 270681 and 290981. These changes indicate a steady growth from autumn to winter with some further, slight growth in spring.

Overall abundances are high on 291281, with the influx of 0 mm animals, and decrease over the following seasons to be lowest in spring. Thus *Cylichnina* shows a clear summer recruitment with growth of animals extending until winter/spring while overall numbers decrease.

3.3.13 *Nassarius*

For convenience the size frequency distribution (Fig. 3.29) was separated into 2 groups, represented by equal numbers of size classes:

Group 1 (0 - 7 mm)

Small *Nassarius* are most common in summer although the low numbers make conclusions tentative.

Group 2 (8 - 15+ mm)

There are no significant changes in mean size (Fig. 3.30) with respect to distance and season, although size does appear to be slightly greater in spring and summer. Animals are too well spread throughout the size classes to make skewness a reliable index.

Overall abundances increase from a summer low through autumn to a winter high before decreasing in spring. Recruitment of *Nassarius* may commence in late summer.

3.3.14 *Austrocochlea*

Although numbers are low throughout the year, there are suggestions of an

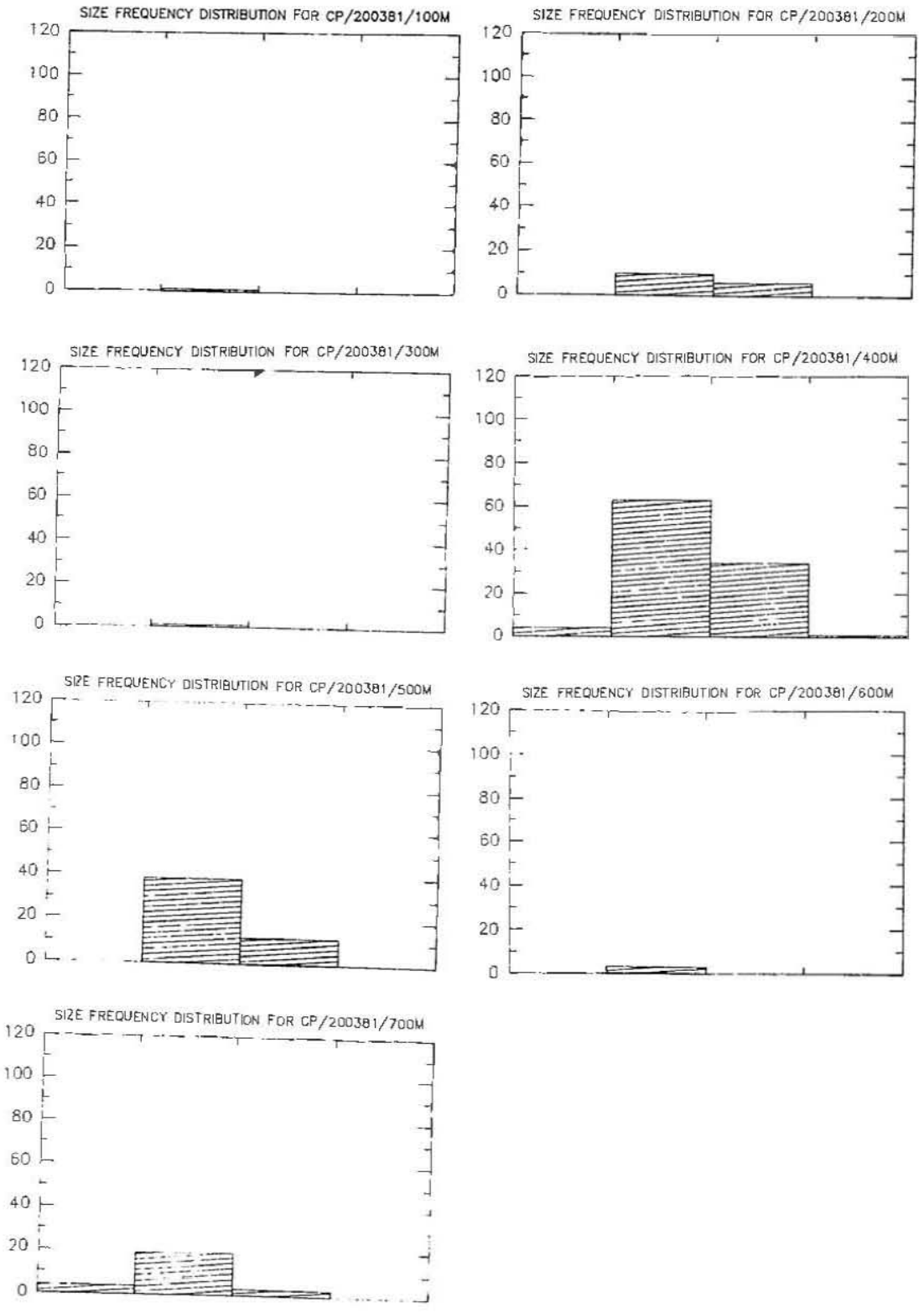


Fig. 3.27 Size frequency distributions of *Cylichnina* at dispersion transect stations. Size class axes range from 0 mm to 3+ mm in 1 mm intervals.

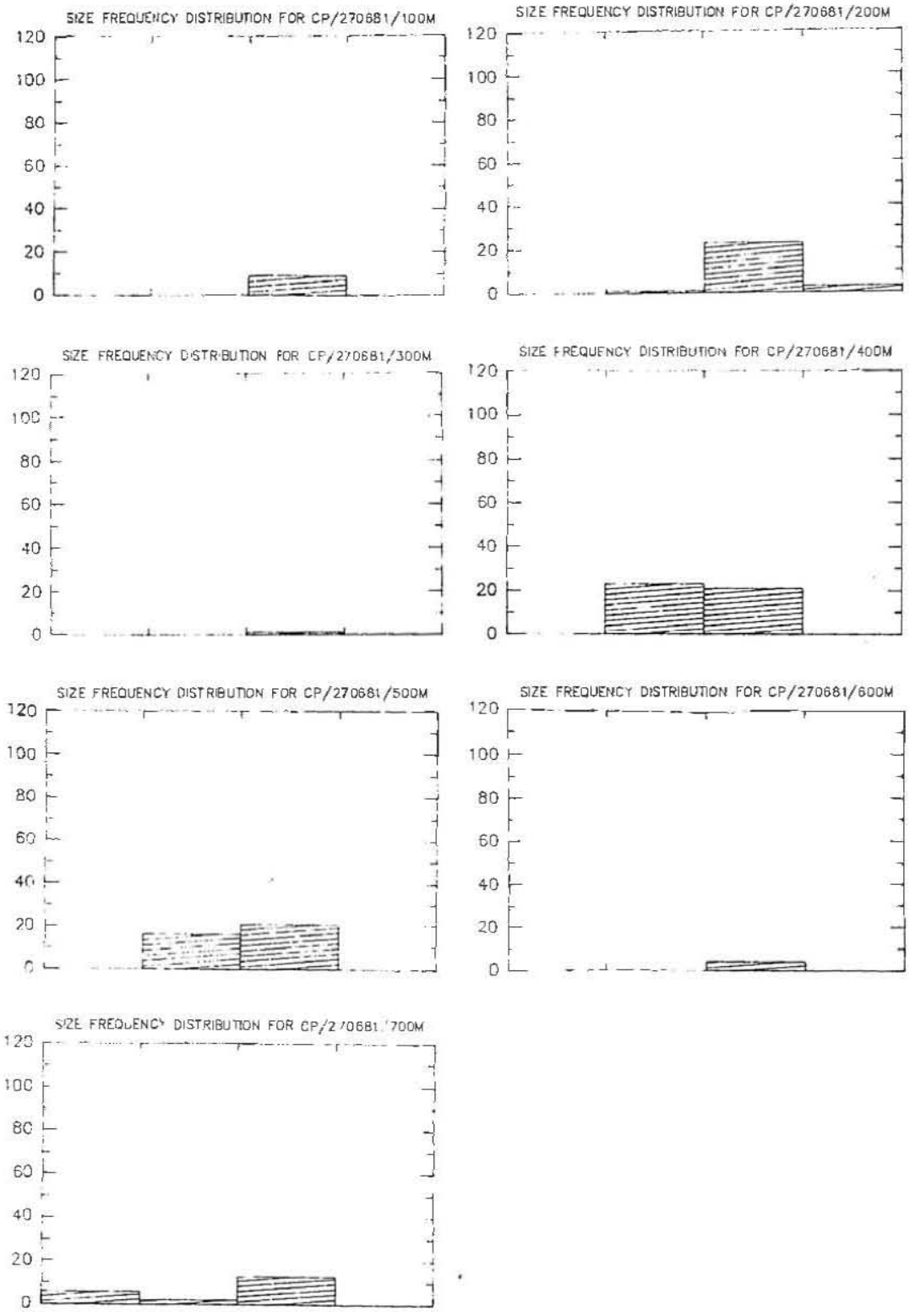


Fig. 3.27 (continued)

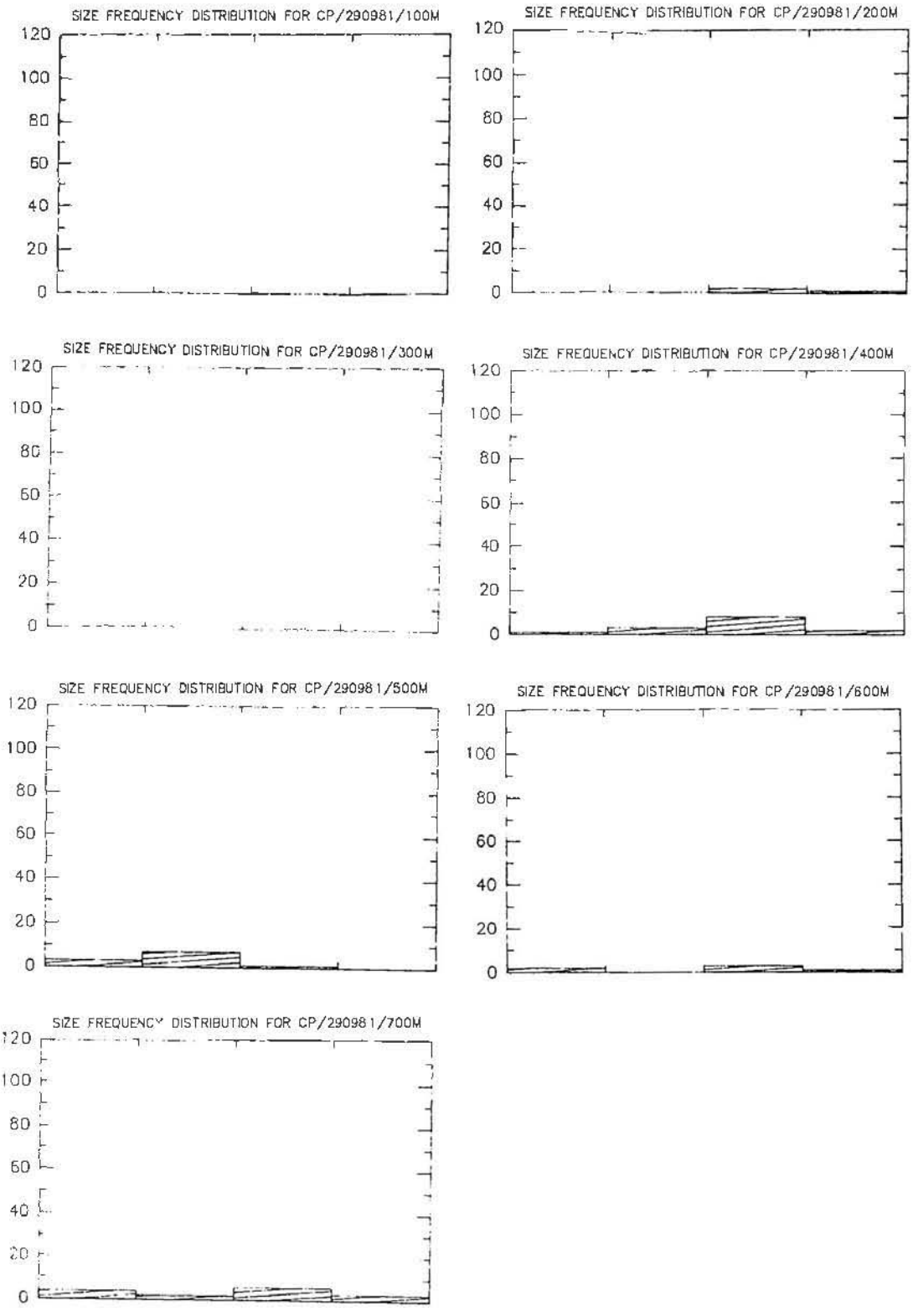


Fig. 3.27 (continued)

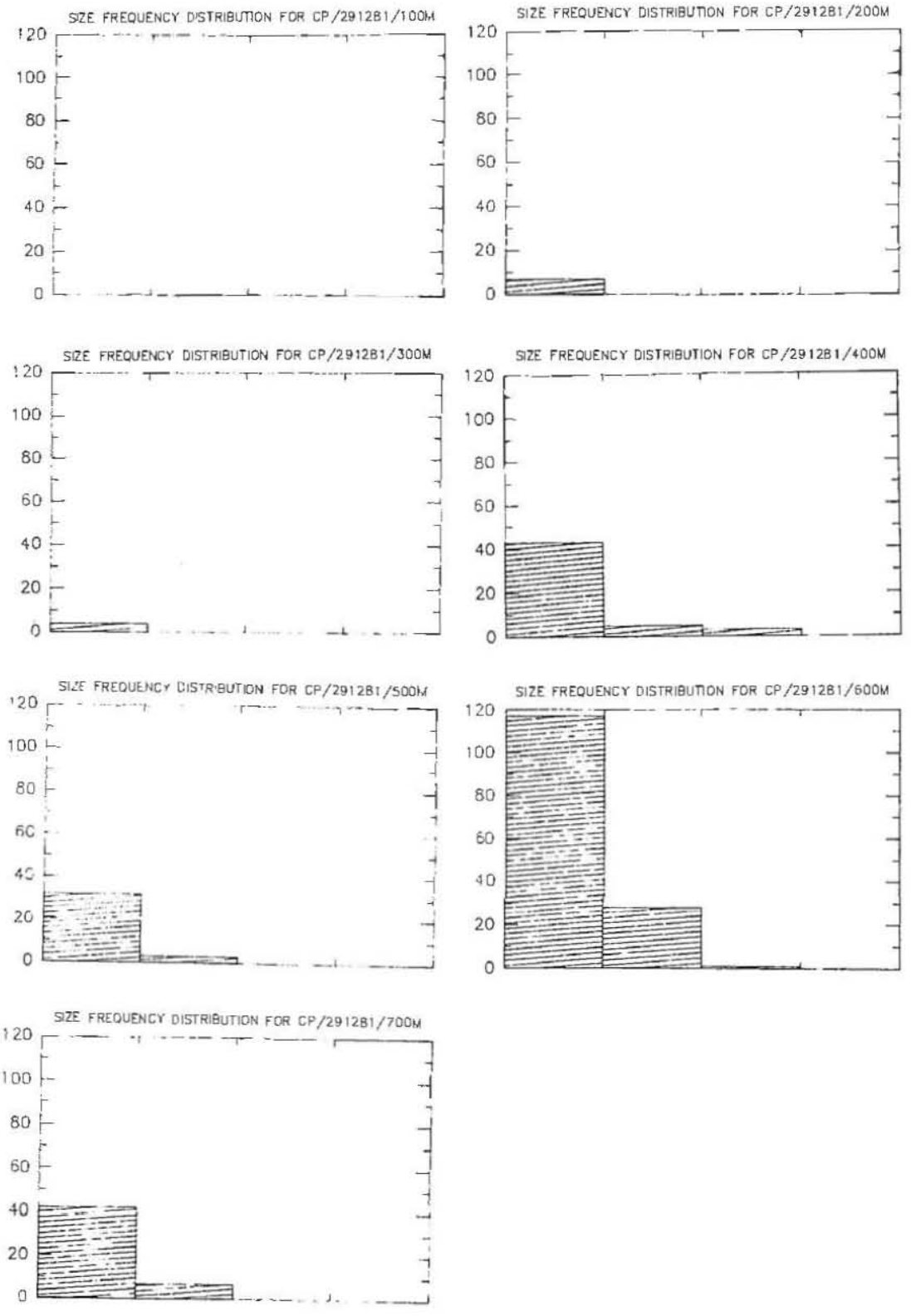


Fig. 3.27 (continued)

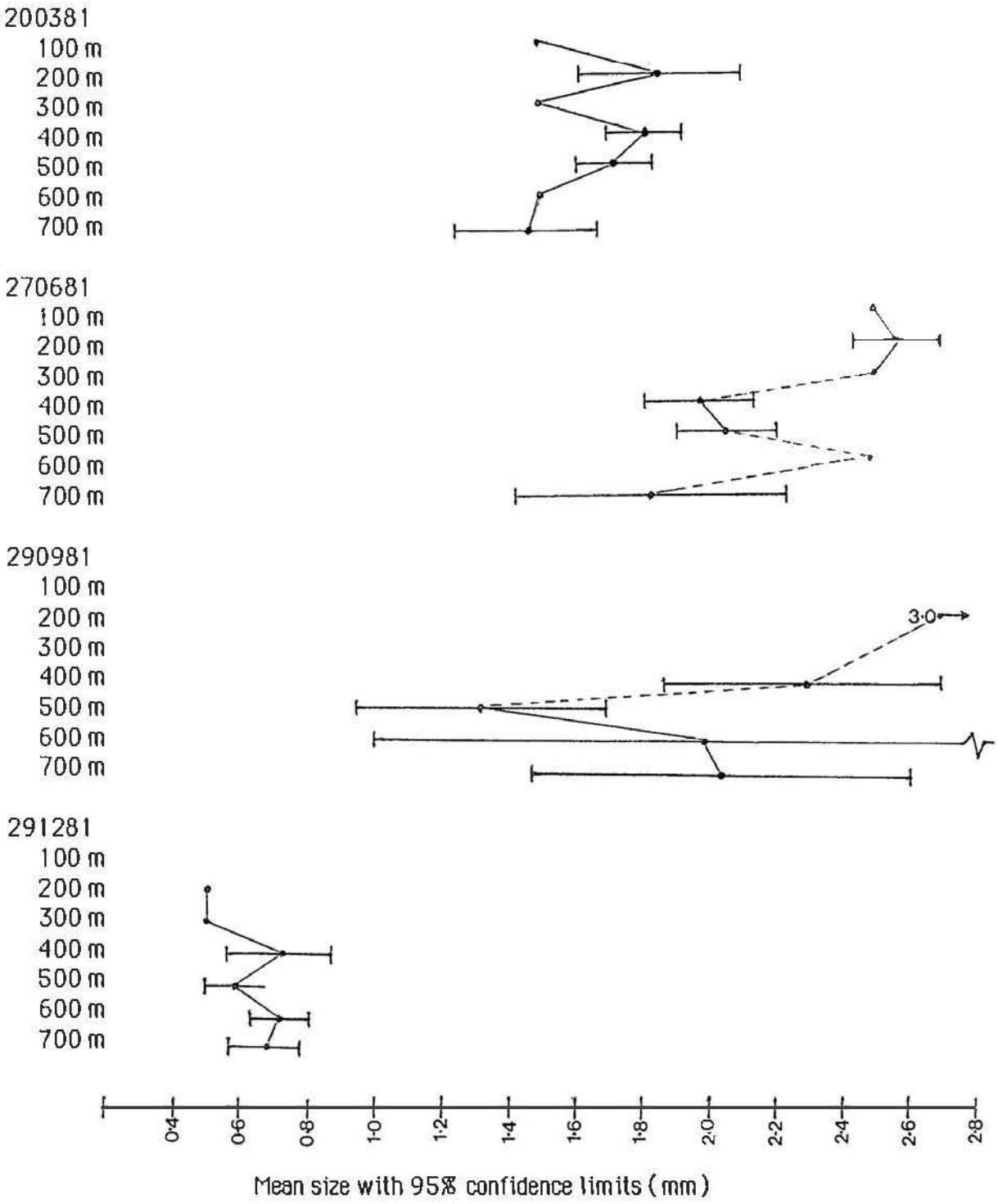


Fig. 3.28 Changes in the mean size of *Cylichnina* over the transect and through the seasons.

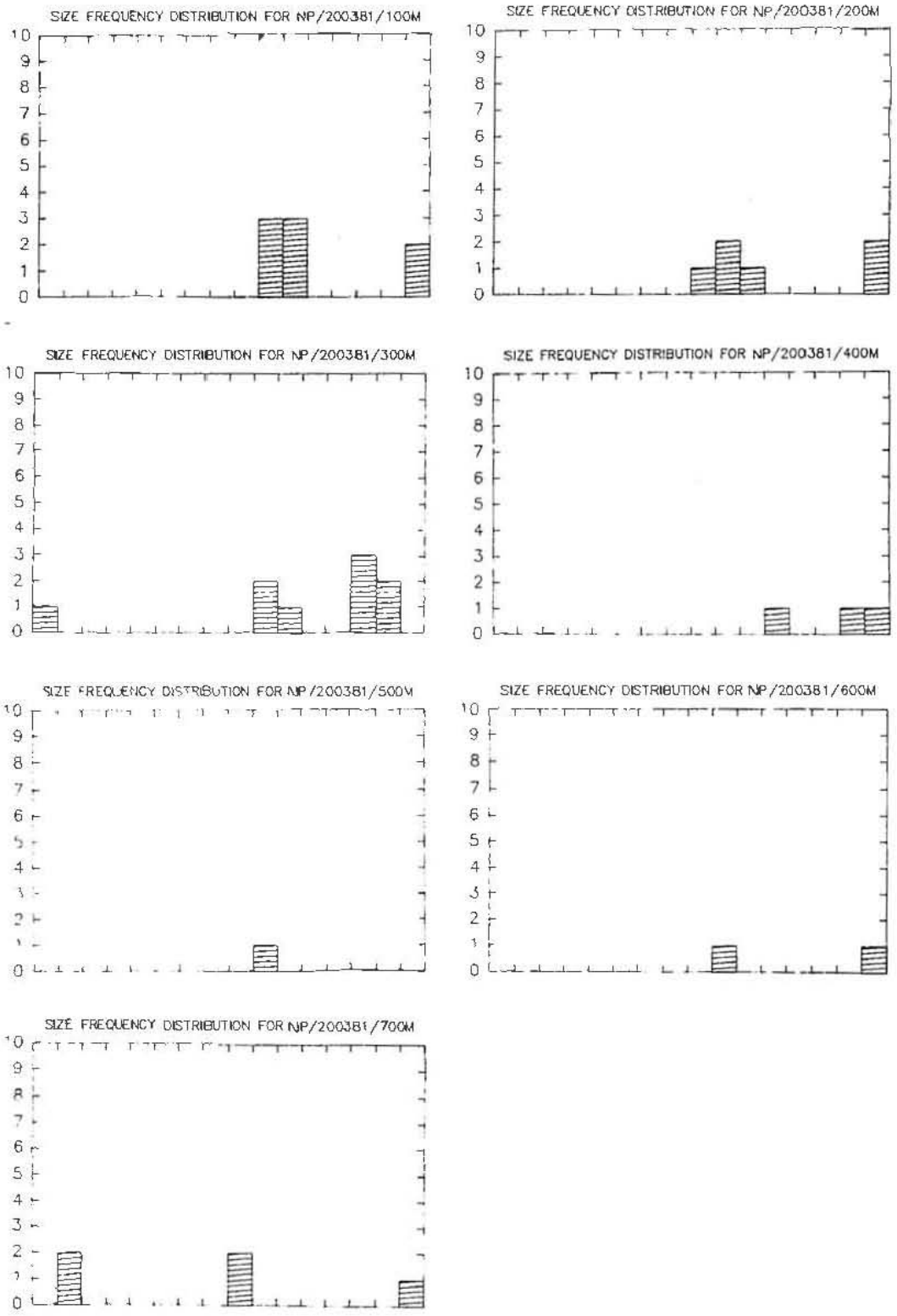
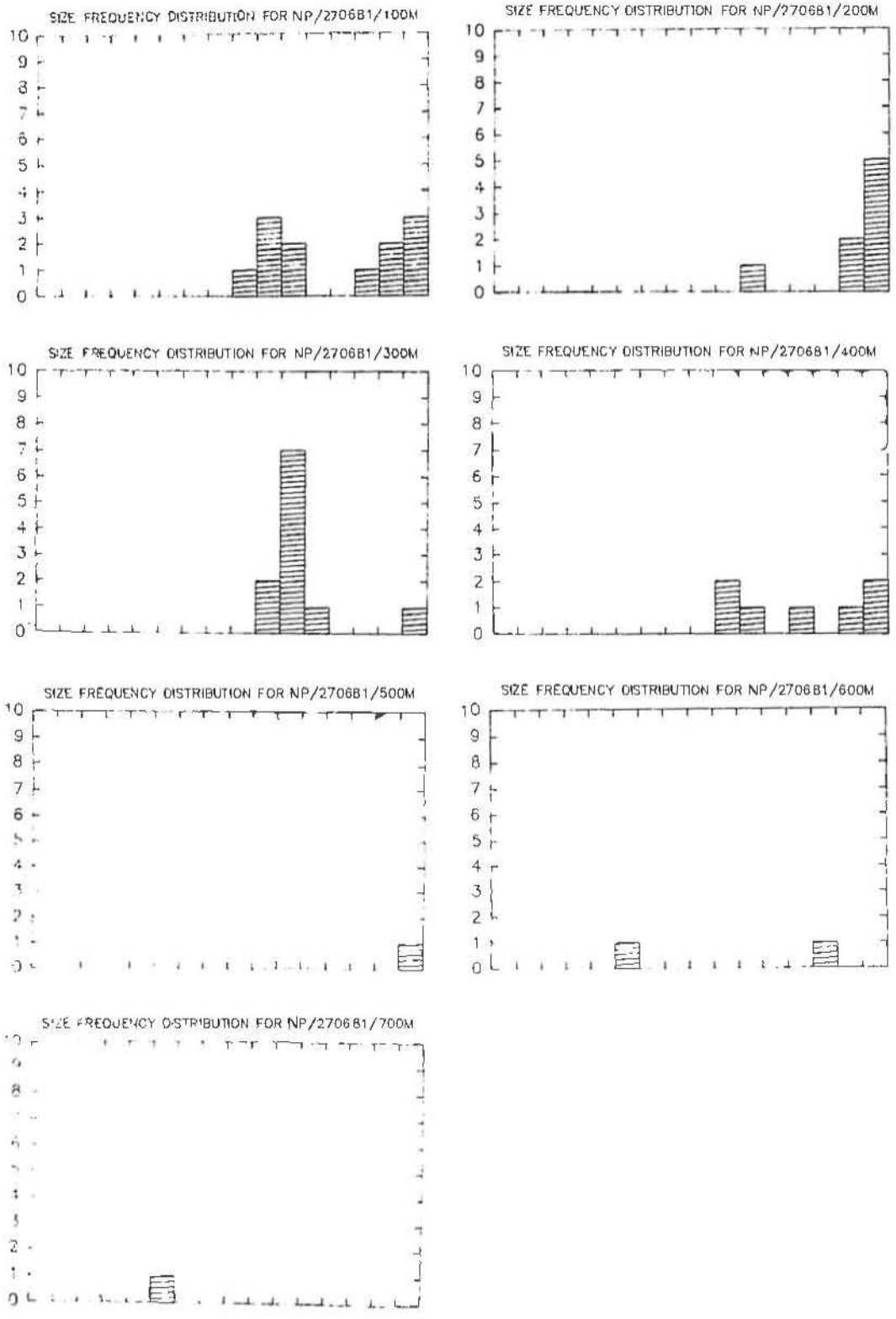


Fig. 3.29 Size frequency distributions of *Nassarius* at dispersion transect stations. Size class axes range from 0 mm to 15+ mm in 1 mm intervals.



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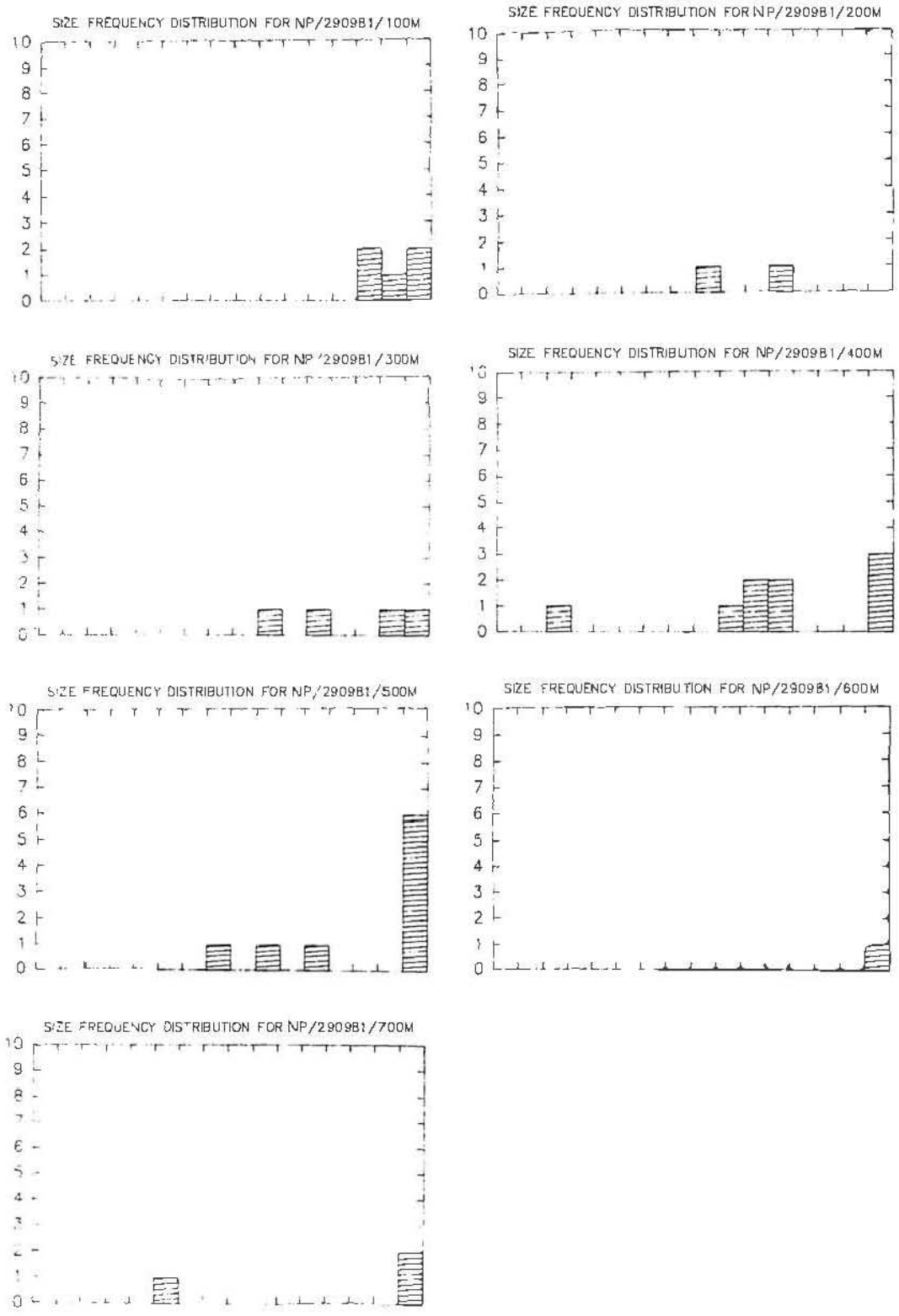

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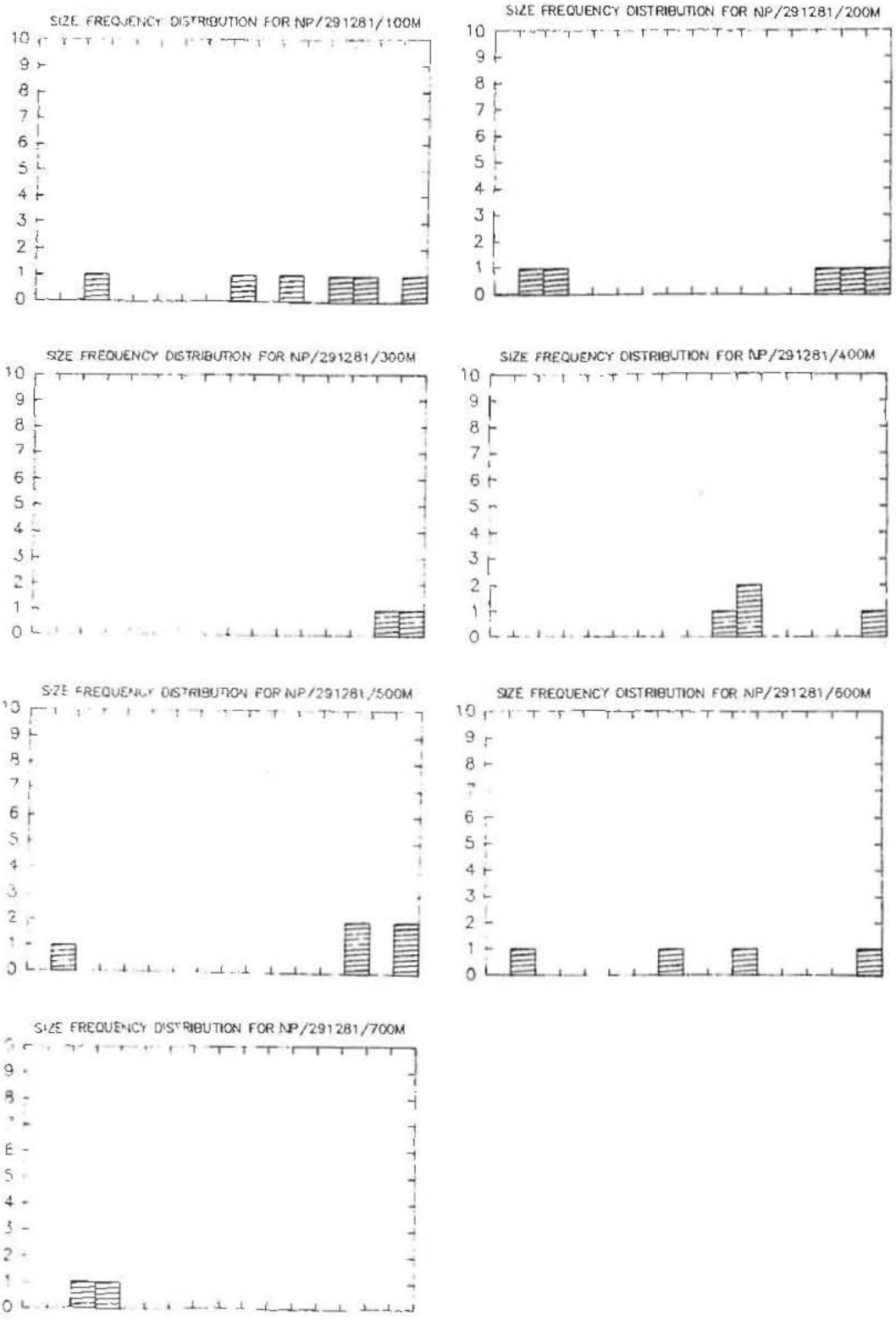

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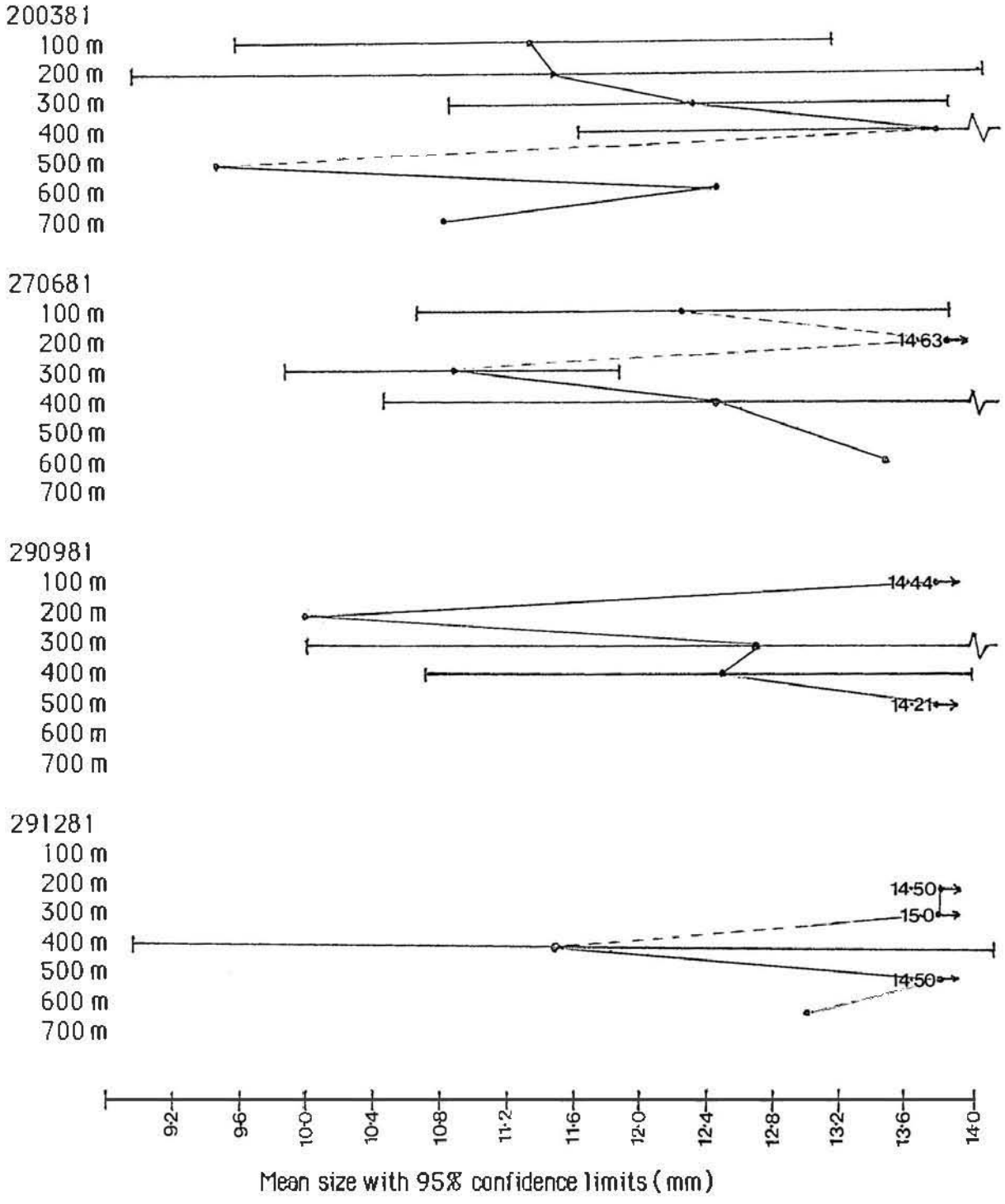


Fig. 3.30 Changes in the mean size of *Nassarius* group 2 animals over the transect and through the seasons. Dotted lines indicate significant differences at 5%.

autumn/winter recruitment. Overall numbers are higher in those seasons and there are a few small animals in the samples. Only large *Austrococchlea* were found in summer.

3.3.15 *Microdiscula*

Microdiscula is found high on the beach throughout the year. Numbers are highest in autumn and decrease over the year to reach a low in summer, indicating autumn recruitment.

3.3.16 *Anthopleura*

Two factors complicate the analysis of the size frequency distributions (Fig. 3.31) of *Anthopleura*. Firstly, *Anthopleura* has no hard body parts which means growth is not necesssarily a one way process. A decrease in the mean size with time could result from a reduction in body size of individual animals rather than a relative increase in the number of young animals.

Secondly, *Anthopleura* is dependent on its hosts, *Anapella* and, to a lesser extent, *Katelysia*, for substrate. The abundance and distribution of *Anthopleura* is therefore inevitably correlated with group 2 *Anapella* and group 2 and group 3 *Katelysia*.

The size frequency distribution of *Anthopleura* was treated as a single group. The general trend is for mean sizes (Fig. 3.32) to be slightly larger on 200381 and 290981 than on 270681 and 291281. None of the changes are statistically significant, however. Although there are large deviations from zero skewness at 600 m and 700 m, the low numbers at those distances make skewness an unreliable index. More reliable skewness indices occur at 400 m on 290981 (negative), 300 m and 400 m (positive), 200 m on 200381 (positive) and 500 m on 270681 (positive).

Abundance patterns are very similar on 270681 and 291281. On 200381 numbers increase high on the beach (200 m). Numbers decrease low on the beach (400 m and 500 m) on 290981. The high numbers at the top of the beach on 200381 comprise relatively large animals. In contrast, the increase in numbers low on the beach, from 290981 to 291281, is accompanied by a decrease in size.

Although small animals are always rare, it appears that recruitment of *Anthopleura* occurs low on the beach (400 m and 500 m) in summer. These animals grow to reach their largest size in autumn. In that season there is an increase in animals high in the beach. The large size of those animals suggests a period of very rapid growth following an early autumn recruitment that was missed by the 291281 sample.

Anthopleura mean sizes drop slightly from autumn to winter but the concomitant decrease in abundance at 200 m suggests this is probably not due to an influx of young animals. Rather, it may be that poor nutrition over winter leads to a decrease in body size

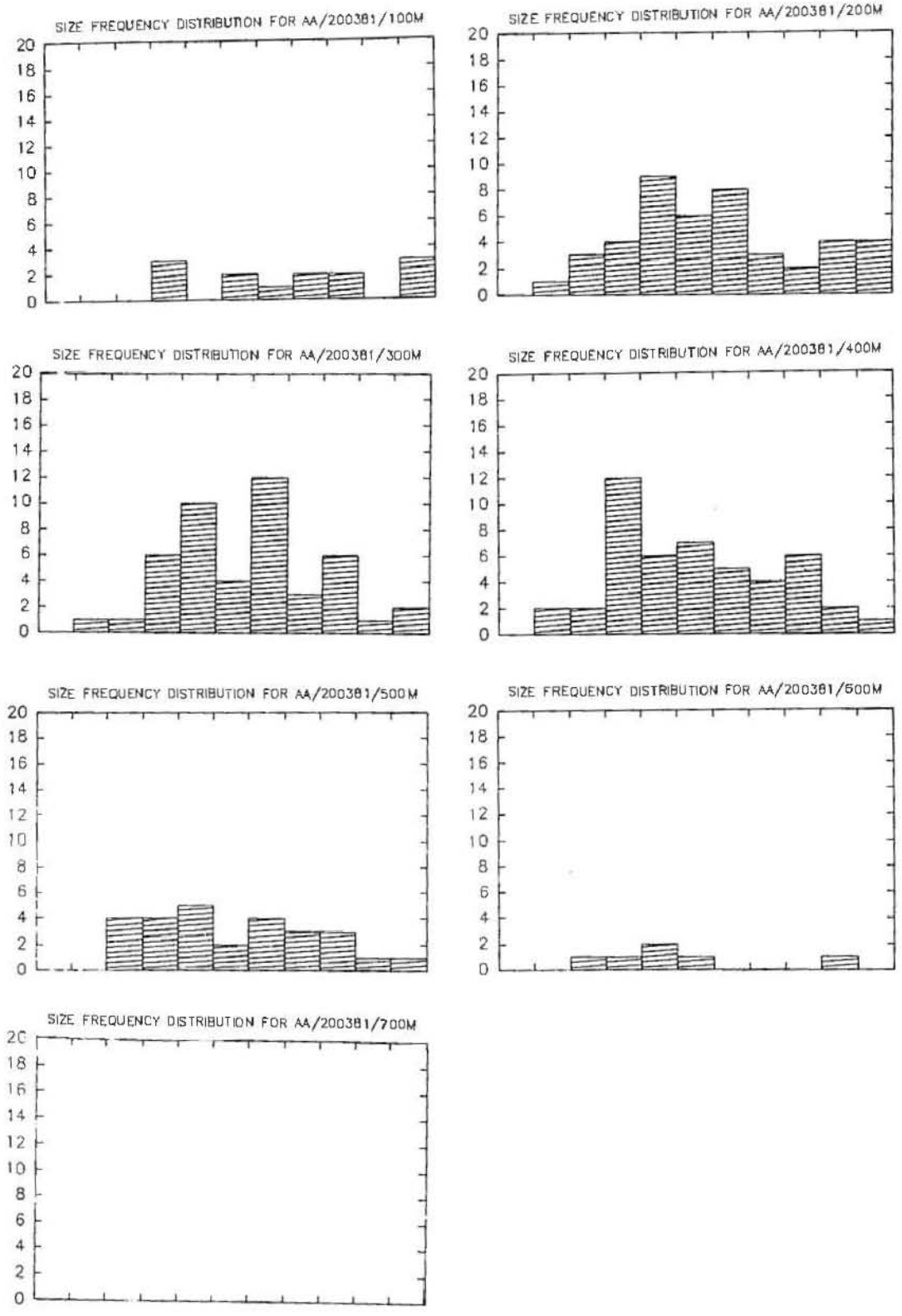
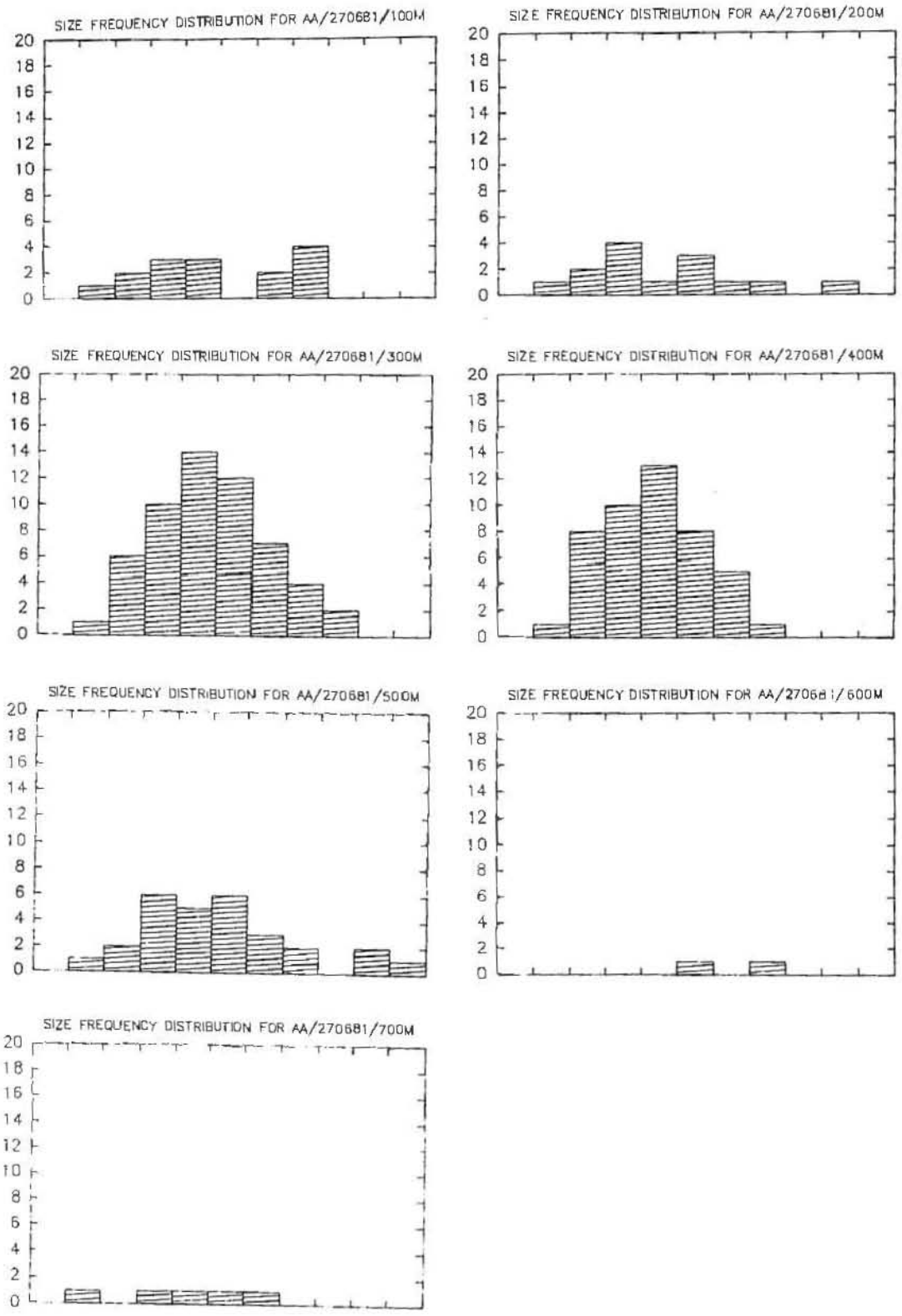


Fig. 3.31 Size frequency distributions of *Anthopleura* at dispersion transect stations. Size class axes range from 0 mm to 10+ mm in 1 mm intervals.



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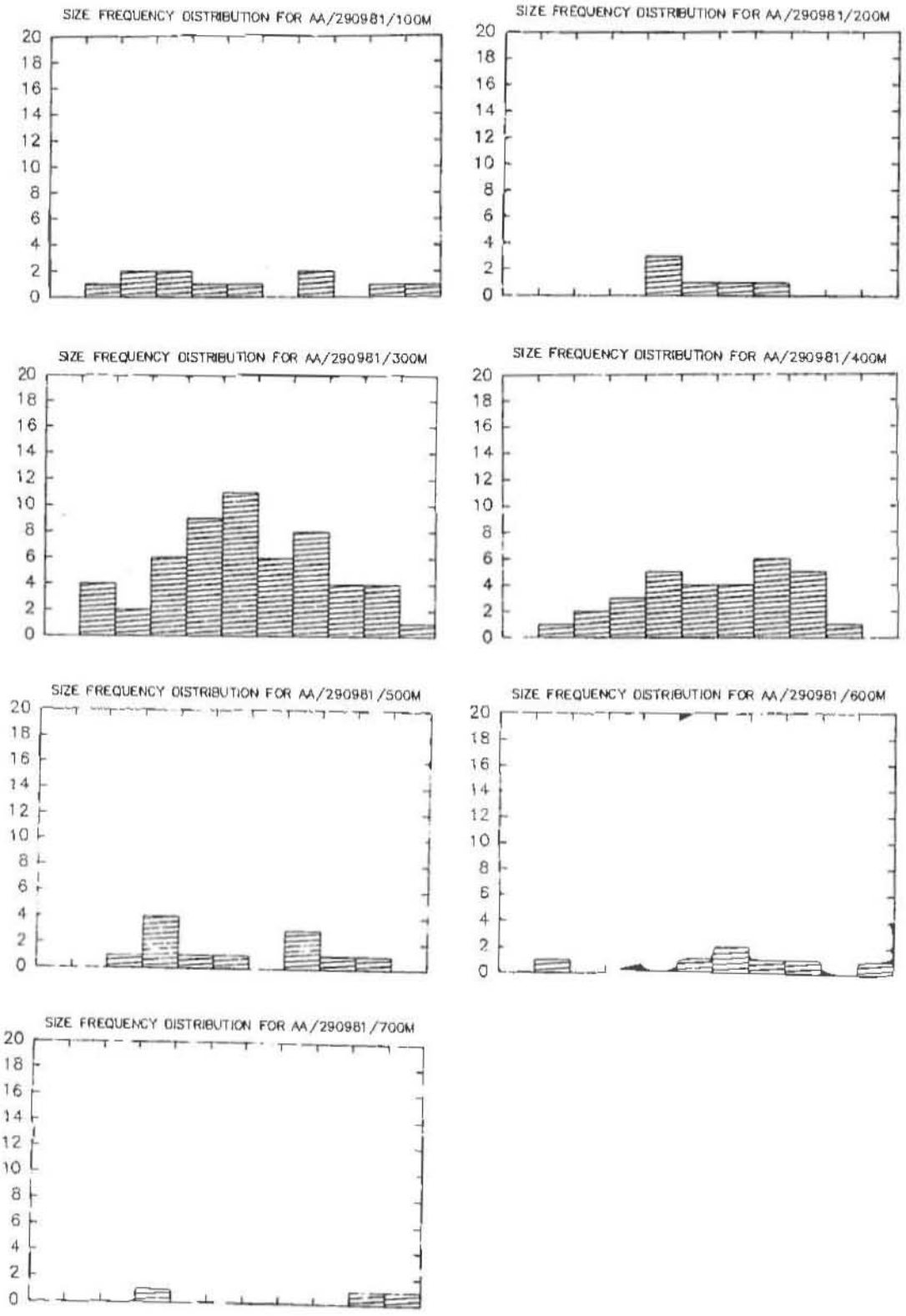

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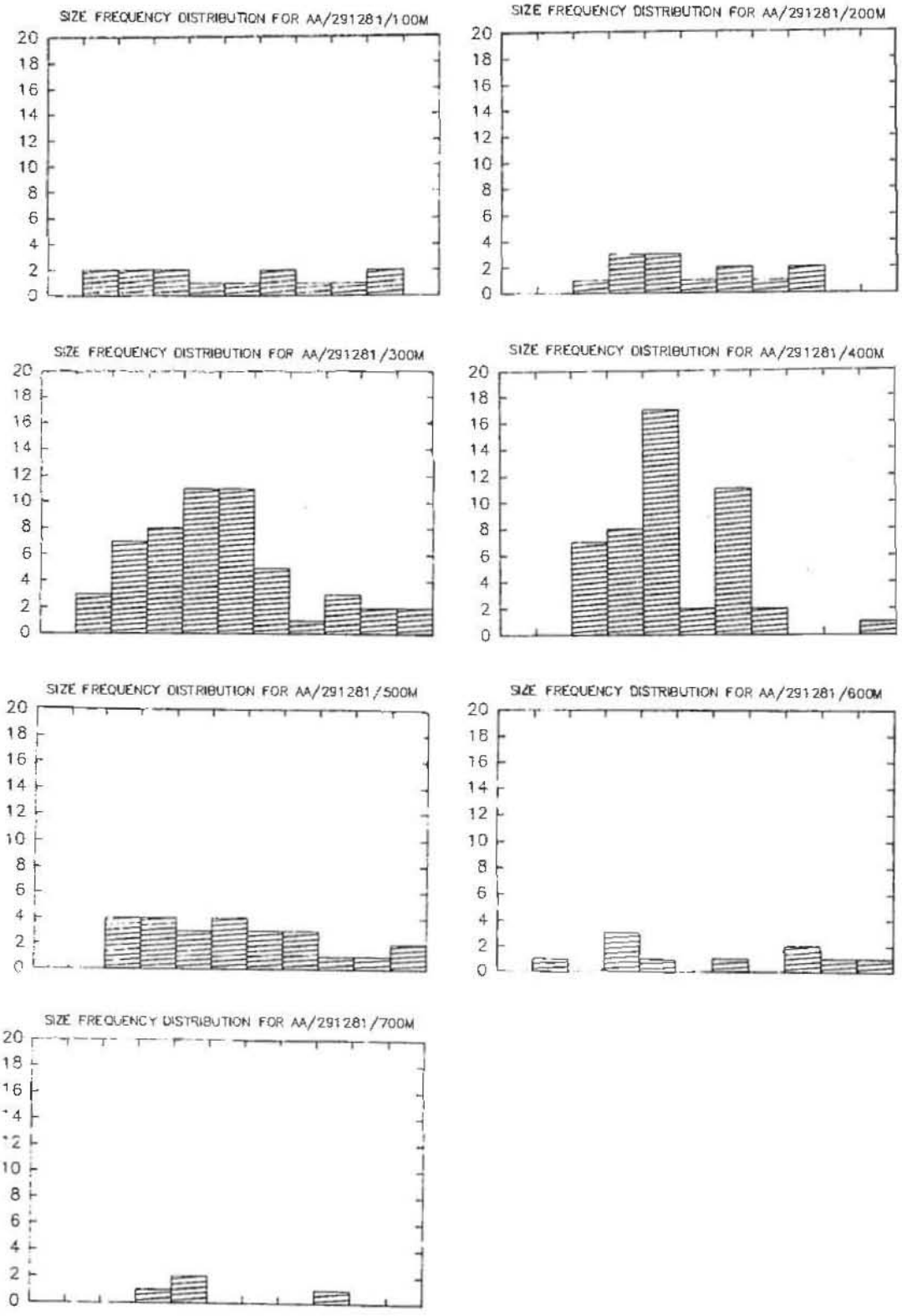

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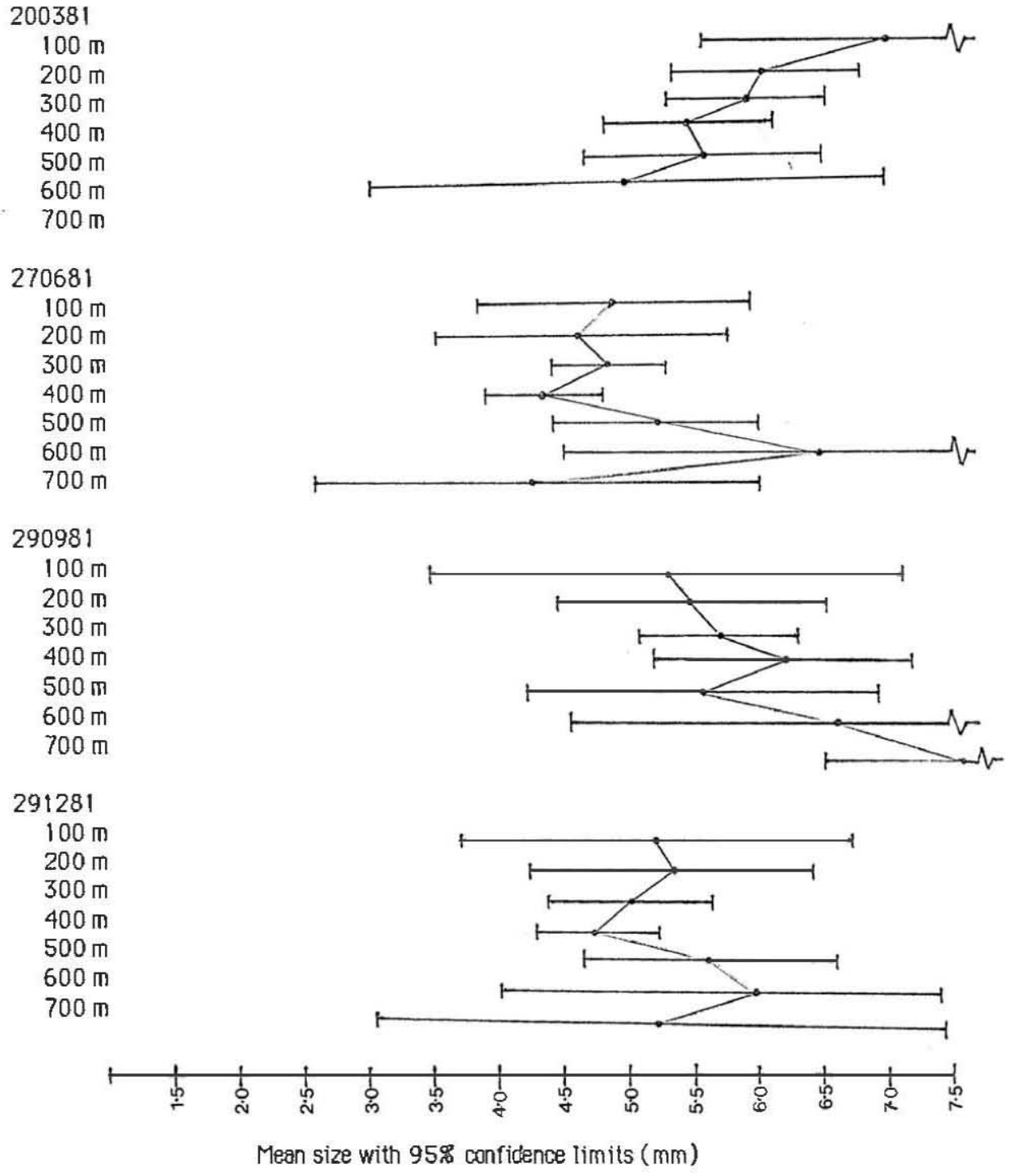


Fig. 3.32 Changes in the mean size of *Anthopleura* over the transect and through the seasons.

of individual animals. The opposite process may explain the suggested rapid autumn growth of the 200 m early autumn recruitment.

The autumn increase in abundance high on the bech may also be related to the autumn increase of *Anapella* group 2 animals which are the principal hosts of *Anthopleura* in that beach zone.

Recruitment of *Anthopleura* , then, probably occurs in summer low on the beach and there may be an early autumn recruitment high on the beach.

3.4 Discussion

3.4.1 Introduction

The molluscs at Pipe Clay Lagoon show reproductive patterns that vary both between and within species, according to their position on the beach. While the bivalves tend to show the greatest recruitment over the cooler part of the year, the gastropods show considerable variation in the seasons of maximum recruitment (here recruitment is taken to be spat settlement). Active migration and/or passive redistribution after spat settlement have not been examined in this study.

The dominant bivalves, *Anapella* and *Katelysia* , and also the dominant gastropods, *Hydrococcus* and *Zeacumantus* , show evidence of continuous recruitment. This, particularly for the bivalves, contrasts with higher latitude species and is probably a consequence of the comparatively mild conditions in Tasmanian waters. Bivalve larvae are abundant in the plankton of Tasman Sea (New Zealand) waters throughout the year while larvae are scarce in northern European weaters over winter (Booth 1983).

Latitude has been shown to influence the duration of bivalve spawning, even within a single species. The cockle, *Cerastoderma glaucum* , for example, spawns in summer and autumn in low latitudes (Ivell 1979) while high latitude populations have a single, summer spawning (Rygg 1970). *Anomalocardia* , the tropical ecological equivalent of European temperate *Cerastoderma* , has continuous settlement of spat (Morton 1978). Among mytilids in Western Australia, southern species tend to be winter/spring breeders at the northern limit of their distribution while in the same region, northern species (at their southern limit) tend to be summer/autumn breeders (Wilson and Hodgkin 1967).

Gastropods appear to be more independent of environmental conditions than bivalves and recruitment patterns can vary between closely related species in the same habitat. Hannaford-Ellis (1983), for example, found that of four sympatric *Littorina* populations in North Wales, two species bred in late summer/early autumn, one bred in spring/summer and the fourth bred throughout the year.

The Gastropoda generally have internal fertilisation, in contrast to the more primitive condition of external fertilization found in the majority of the Bivalvia (Purchon 1968). Gastropods are thus frequently able to provide embryonic protection, usually in the form of a protective coating. Rather than expending reproductive energy by producing large numbers of gametes, gastropods often divert the energy into brood care for a smaller number of embryos. Gastropods are more selective about when and where the eggs are deposited.

3.4.2 The bivalves

The general lack of brood care shown by the Bivalvia is largely responsible for their

greater dependence on environmental conditions for determining the onset and success of reproduction in that group. This is exemplified by the recruitment patterns of *Anapella*, *Katelysia*, *Soletellina* and *Wallucina*.

Since planktonic larvae were not sampled (for any species), it is not known to what extent the recruitment patterns reflect the underlying patterns of reproduction. The relatively constant numbers of *Anapella* 0 mm animals at 400 m, however, suggest that, its reproductive effort may be constant while actual reproductive success varies with the seasons and position on the tidal flat.

For *Anapella*, 400 m appears to be a pivotal area with respect to reproduction. The beach profile either side of 400 m increases in height (until 500 m on the low water side) making both sides subject to greater desiccation than the central (400 m) point. Numbers of 0 mm animals are high throughout the year at 400 m and the autumn/winter recruitment wave moves from 400 m up (and to a lesser extent down) the beach. It appears that reproductive success is a function of both beach height and season, with low beach areas and cool seasons aiding juvenile survival.

Katelysia also shows a wave of recruitment that moves up the beach during the cooler months. There are differences between the *Anapella* and *Katelysia* recruitment waves, however, and these appear to be related to the preferred zones of the two species. While *Anapella* adults are found throughout the upper beach, *Katelysia* adults, individuals greater than c. 10 mm (Mane 1976: *Katelysia opima*) are generally restricted to areas below 300 m, suggesting a lower tolerance to desiccation in that species.

Following summer, *Anapella* recruitment increases quickly above 400 m and reaches a maximum by winter, which is maintained through spring. High-beach recruitment of *Katelysia* lags behind that of *Anapella*, possibly by as much as a season and peak recruitment is not reached until spring. *Katelysia* does not show constant reproductive success at the lower end of its zone, despite the less exposed conditions there.

Katelysia, then, with its low-beach zonation and variable recruitment success in all sections of the beach, appears to be less tolerant of desiccation than *Anapella*. The high abundance of *Katelysia* 0 mm animals at the lowest station (700 m) in autumn, compared to higher beach areas, highlights a probable desiccation related decline in numbers over summer.

While *Anapella* appears to have constant reproductive effort (as distinct from success), reproductive effort in *Katelysia* is variable. Other members of the Veneridae are known to spawn during spring and summer, including *Venerupis pullastra*

(Quayle 1952) and *Chione stutchburyi* (Booth 1983). *Katelysia opima* has a major spawning season in October in India (Mane 1976) but comparison with the temperate *K. scalarina* is difficult. *Katelysia scalarina* probably has a peak spawning period in spring.

Unfortunately, there appears to be no information on spawning patterns in other Donacillidae to allow comparison with *Anapella*.

Although large *Anapella* individuals are found throughout most of the upper beach, numbers are least variable at 300 m and 400 m and this supports the hypothesis that 400 m could be a 'refuge' area for *Anapella*. The longer periods of immersion at this distance, compared to high-beach areas, may account for this.

Living in the intertidal area typically requires energy compensation mechanisms (Gillmor 1982). Filter feeders, in particular, must assimilate food more rapidly and efficiently to compensate for the reduction in feeding time. A combination of energy conserving mechanisms and energy supplementation mechanisms generally make approximately equal contributions towards compensating for the restrictions placed on high-level intertidal species (Gillmor 1982). The high energy cost of growth and reproduction, however, may result in a decrease in production (in terms of both somatic and shell growth and gamete formation) with increasing shore height in many species (Griffiths 1981a,b). *Anapella* may maximise the benefits of low shore living by retaining the small but constant population of relatively large animals at the low-beach end of its zone. Those animals appear to produce large numbers of offspring through much of the year. Reproductive effort has been shown to increase with size in bivalves (e.g. Griffiths and King 1979; Thompson 1979) and large *Anapella* breeding almost continuously could quickly come to dominate the beach numerically. The low numbers of large *Anapella* may be the result of competition with *Katelysia* adults; this will be examined in later chapters. Newly settled *Anapella* may benefit from reduced competition high on the beach and they do grow rapidly there, although not to large sizes.

Similar tide-related trophic factors could account for the significantly greater body size attained by *Katelysia* in the low beach areas, both within that species and in comparison to *Anapella*. *Katelysia* does not show a constant population of large animals, however, although their numbers are lower and less variable near 300 m and 400 m. This could be due to a buffering effect of competition with *Anapella*. Growth rates of *Katelysia* appear to be highest at 600 m and 700 m, again probably due to increased feeding time.

The different reproductive strategies of *Anapella* and *Katelysia*, together with the

apparent differences in desiccation tolerance, probably account for much of the numerical dominance of *Anapella*.

Zonation and recruitment patterns also appear to be related in *Soletellina* and *Wallucina*. Like *Katelysia*, both species are most abundant below 300 m and both also show peak recruitment in the cooler months. *Soletellina* also shows evidence of a wave of 0 mm recruitment up the beach in winter and has continuous (but variable) settling in low areas. *Wallucina*, however, never showed a high abundance of 0 mm animals in the sample.

3.4.3 The gastropods

Similar factors operating on the principal gastropods may be responsible for much of the numerical dominance of *Hydrococcus* in comparison to *Zeacumantus*. Like *Anapella* and *Katelysia*, *Hydrococcus* and *Zeacumantus* appear to have continuous reproduction, with recruitment being most successful at the low-beach ends of their respective zones. In some respects, the seasonal changes in recruitment of *Hydrococcus*, below 400 m, match those of *Katelysia*. Both species have low recruitment in autumn which increases over winter to a spring maximum before the summer decline. *Zeacumantus*, however, shows a sharp increase in recruitment from a summer low to an autumn maximum before recruitment declines over winter and spring.

Hydrococcus is known to have protective mechanisms for its developing embryos. Usually, a single embryo develops in an egg capsule and the young hatch as crawling juveniles (Wells and Threlfall 1982a). Despite this protection, seasonal variation in recruitment is considerable in Pipe Clay Lagoon. This contrasts with the findings of Wells and Threlfall (1982b) for *Hydrococcus* in Peel Inlet, Western Australia, where they observed steady recruitment over 2 years. The differences may, at least partly, be accounted for by different sampling procedures. Wells and Threlfall did not consider animals that passed through a 1 mm mesh; also, samples were only taken from one station. That station was never recorded as being exposed, although the possibility of exposure betweeen sampling dates was pointed out.

The comparison with the results of Wells and Threlfall (1982 a, b), therefore, would best be made with the 600 m and 700 m stations and 1 mm animals at Pipe Clay Lagoon. *Hydrococcus* does show steady numbers of 1 mm animals at those stations between autumn and spring but there is a marked increase in abundance in summer, due to the growth of the 0 mm animals recruited in spring.

Since the 600 m and 700 m stations at Pipe Clay Lagoon were frequently exposed, it is likely that they lie higher in the intertidal zone than the station sampled by Wells and

Threlfall. This may explain the differences in recruitment patterns; almost continuous submersion would buffer seasonal changes in environmental conditions in the intertidal region.

Hydrobia, the northern hemisphere ecological equivalent of *Hydrococcus* (Ponder 1982) also shows seasonal variation in recruitment. Anderson (1971) observed the greatest number of *Hydrobia ulvae* in the 0 mm size class in autumn, following a peak of egg capsule deposition over spring and summer. Animals in the 1 mm size class appeared to be most abundant in the (following) summer; Wolff and de Wolff (1977) made similar observations for 1 mm animals.

Hydrobia appear to be slower growing in northern Europe than *Hydrococcus* is in southern Australia. While A.Anderson (1971) suggests that *Hydrobia* does not reach full maturity until an age of almost 2 years, *Hydrococcus* requires only 4 months to mature in Peel Inlet (Wells and Threlfall 1982b).

To summarise, in Pipe Clay Lagoon *Hydrococcus* shows a combination of the characteristics of the northern European *Hydrobia* and the south west Australian *Hydrococcus*. Like *Hydrobia*, *Hydrococcus* in Pipe Clay Lagoon probably has peak reproductive activity in spring; *Hydrococcus* shows no marked peak in Peel Inlet (Wells and Threlfall 1982b). In both Peel Inlet and Pipe Clay Lagoon, *Hydrococcus* exhibits rapid growth, with Pipe Clay Lagoon animals entering the 2 mm class (=maturity, Wells and Threlfall 1982b) by the first summer; *Hydrobia* requires 3 summers to reach maturity (Anderson 1971). The slower growth of *Hydrobia* is highlighted by an almost complete cessation in winter (Wolff and de Wolff 1977). By the first winter in Pipe Clay Lagoon, *Hydrococcus* has approached the maximum size; this takes 7 to 8 months in Peel Inlet (Wells and Threlfall 1982b) making growth rates in the two areas comparable.

Zeacumantus diemenensis, like other Potamididae, probably protects its embryos in egg masses with the young hatching as crawling fry as they do in *Z. subcarinatus* (Pilkington 1974). In Pipe Clay Lagoon, *Z. diemenensis* is primarily restricted to the upper half of the beach and it could be expected to show more specialised reproductive patterns than the widely distributed *Hydrococcus*.

While both species show continuous recruitment of 0 mm animals, *Zeacumantus* does appear to have a definite onset of peak recruitment in autumn. In New Zealand, *Z.subcarinatus* egg production occurs over summer (Graham 1941) and the autumn recruitment of *Z. diemenensis* suggests that it may also have summer egg production. A related species, *Velacumantus australis*, also breeds over summer and autumn (Ewers 1963). In Pipe Clay Lagoon, the autumn cohort of *Zeacumantus* grows slowly

over winter and spring prior to a period of rapid growth the following summer.

The Amphibolidae, which include *Salinator*, are exceptional among all Pulmonata in that they possess an operculum (Hubendick 1978). *Salinator* is tolerant of desiccation and, although it requires regular immersion in seawater, animals are often found high in the supralittoral zone (Smith and Kershaw 1979). The reproductive strategies of *Salinator* would therefore be expected to reflect adaptations that allow the desiccation effects to be overcome.

Related species, such as *Amphibola* and *Siphonaria*, have capsulate veligers (Morton 1979) but there appear to be no detatiled studies of reproduction in *Salinator*. Creese (1980) found *Siphonaria denticulata* to have a long breeding season (in New South Wales), extending over early summer and autumn. In Pipe Clay Lagoon, recruitment of *Salinator* also appears to be extended, although reproduction probably commences in early spring and declines over summer.

Bembicium and large *Salinator* share a similar high-beach zonation. *Bembicium auratum*, like the closely related *B. nanum*, has partly pelagic development, with benthic egg masses giving rise to pelagic larvae (Mileikovsky 1975). *B. melanostoma*, which is found in high intertidal, stenohaline mudflats, produces young that hatch at the crawling stage (Anderson 1958). All three species appear to reproduce in (late) winter and spring (*B. nanum* : Anderson 1961, Underwood 1974; *B. auratum* : Anderson1962; *B. melanostoma* : Anderson 1958) although Underwood (1974) found *B. nanum* to continue spawning through summer. *B. auratum* retains the primitive habit of spawning in pools (Anderson 1962), suggesting a lack of larval tolerance to desiccation, despite the high-shore habitat of the adults. From the small number of juvenile *Bembicium* found in the dispersion transect samples, a winter/spring reproduction in Pipe Clay Lagoon is probable. Young (2 - 3 mm) animals are most common in autumn and these probably grow over summer after a spring hatching.

The Rissoidae, the family to which *Rissopsis* belongs, show highly tractable recruitment patterns. In northern European waters the main settlement period of the planktotrophic veligers is spring (Frettler and Shale 1973; Wigham 1975) although Wigham (1975) also observed that *Rissoa parva* recruitment peaks in late summer and late autumn, with overall numbers being lowest in winter.

Rissoa settlement is very dependent on the algal substrate; on poorly structured algae *Rissoa* numbers decline during winter while on algal mats, numbers may actually increase during winter (Wigham 1975). Wigham attributed this to the different degrees of shelter afforded by the different algal forms and observed that the seasonal changes in

population size and structure varied according to the algal substrate. Clearly, reproductive success in *Rissoa* is highly variable and the total life span may vary between 4 and 10 months with up to 6 generations per year (Wigham 1975).

In Pipe Clay Lagoon there is a comparative paucity of macroalgae (except for the *Synechococcus / Oscillatoria* mats) although during caging experiments *Cladophora* developed strongly in many long-term cages. With a relative absence of shelter, *Rissopsis* is likely to be more dependent on gross environmental changes than *Rissoa*. This, together with the warmer climate in south-eastern Tasmania, could account for the low abundances of *Rissopsis* in summer.

Agatha probably shares the characteristics of other Pyramidellidae which are typically host-specific ectoparasites; their mode of life is associated with special adaptations of both the feeding and the reproductive structures (Fretter and Graham 1949b; Purchon 1968). The reproductive strategies of the Pyramidellidae also appear to reflect their specialised habits. The eggs are carried on the host animal in an attached jelly mass; egg masses of *Odostomia* have been observed on the scallops *Pecten* and *Chlamys* in summer (Lebour 1932). Other *Odostomia* species are ectoparasitic on sedentary polychaetes and the egg masses are laid close to those hosts (Fretter and Graham 1949a,b) while *Turbonilla rufescens* is associated with a coelenterate (Fretter and Graham 1949a).

With an almost obligatory relationship with their hosts (some species are not strictly host-specific: Cole and Hancock 1955), the Pyramidellidae should show reproductive patterns that are closely linked to those of the hosts. In some areas, for example, *Odostomia scalaris* is found only on juvenile *Mytilus edulis* (Fretter and Graham 1949b) and the population dynamics of both species would necessarily be synchronised.

In Pipe Clay Lagoon, the high shore distribution of *Agatha* suggests that *Anapella* or *Anthopleura* are the most likely hosts. Both *Anapella* (group 2) and *Anthopleura* show an autumn increase in abundance in the *Agatha* zone and the apparent late summer/early autumn recruitment of *Agatha* may be correlated with this. Sedentary polychaete worms and *Katelysia*, which are potential hosts, have a lower zonation. The possible relationships will be examined in later chapters.

Like the Pyramidellidae, the Scaphandridae, including *Cylichnina*, could be expected to show correlations between their reproductive patterns and those of other species. The Scaphandridae are not ectoparasitic but are rapacious carnivores (Macpherson and Gabriel 1962). Many of the Cephalaspidea feed on small bivalves (Macpherson and Gabriel 1962; Rudman 1970) while others feed on juvenile psosobranchs (Smith

1967). The population cycles of cephalaspids preying on juvenile molluscs would be strongly influenced by those of their prey, particularly with respect to the abundance and distribution of newly settled animals. Indeed, *Retusa* is known to selectively feed on newly settled stage of *Hydrobia* and *Bittium* (Rasmussen 1973). The spawning of *Philine gibba* is synchronised to achieve hatching at the time of optium food availability (Seager 1979).

The distribution of *Cylichnina* in Pipe Clay Lagoon is predominantly below 300 m, a zone shared with *Katelysia* and *Hydrococcus* juveniles. Correlations with other mollusc species will be examined in detail in later chapters, but it is possible that the recruitment of *Cylichnina* is linked to the spring recruitment peaks of *Katelysia* and *Hydrococcus* .

Nassarius was found in relatively low numbers in all dispersion transect samples but this belies the actual abundance of that species in Pipe Clay Lagoon. The highly contagious dispersion pattern of *Nassarius* , together with a selective avoidance of *Nassarius* feeding aggregations during the sampling program, meant that few animals were included. There is evidence, however, to suggest that recruitment occurs in summer, as is typical of the Nassariidae (Brown 1982).

Like *Nassarius* , *Austrocochlea* was also uncommon in the samples but there are suggestions of an autumn/winter recruitment. Underwood (1974) observed continuous spawning in *Austrocochlea* , with juveniles being found throughout the year and most commonly in late spring. There are insufficient data to determine whether the observed recruitment pattern of *Austrocochlea* in Pipe Clay Lagoon represents a significant departure from the findings of Underwood (1974).

There have apparently been no studies of the reproductive ecology of the Skeneopsidae. In Pipe Clay Lagoon *Microdiscula* appears to have an autumn recruitment.

3.4.4 The anemone

Intertidal anenomes may exhibit more than one mode of reproduction (Ottaway 1980; Sebens 1982a). *Anthopleura elegantissima* , for example, releases gametes for external fertilization which leads to a late autumn/early winter settlement (Sebens 1981). Following starvation, however, *A. elegantissima* may reproduce by asexual fission, most commonly in autumn and winter when individual anenomes are decreasing in size (Sebens 1980, 1982b). Asexual fission is not a general capability among anenomes, however, and *A. xanthogrammica* never divides asexually, despite its close taxonomic relationship with *A. elegantissima* (Sebens 1980).

It is unlikely that *Anthopleura* reproduces asexually in Pipe Clay Lagoon. Typically

one or two *Anthopleura* were found on each host animal (large *Anapella* and *Katelysia* or, rarely, *Austrococchlea*). Asexual fission would be expected to result in several animals per host. Similarly, *Anthopleura* does not appear to exhibit external brooding, as is found in some anenomes (Dunn 1977).

Anthopleura shows a slight decrease in mean size over winter, probably due to starvation. Seasonal, starvation-induced changes in individual body size are common in intertidal anenomes (Sebens 1980; Ottaway 1979a, 1980). *Telia crassicornis,* for example, can withstand starvation for up to 9 months and show no body growth during that period (Chia and Spaulding 1972). Ottaway (1979a) has described daily fluctuations in *A. tenebrosa* body size, due to tide-related expansion and contraction and rainfall. *A. tenebrosa* body size also appears to be correlated with reproductive condition (Ottaway 1979b). Obviously, little reliance can be placed on seasonal fluctuations in body size as an indicator of recruitment patterns.

Anthopleura shows two deviations from a stable population size during a year in Pipe Clay Lagoon. There is a spring decrease followed by a summer increase below 300 m and an autumn increase above 300 m. In summer there are low numbers of large *Katelysia* below 300 m, making for a relative shortage of *Anthopleura* hosts. Despite this, there is an increase in the abundance of *Anthopleura* . This suggests that there is a genuine *Anthopleura* recruitment below 300 m and concurs with the breeding patterns of other anenomes (Jennison 1979; Ottaway 1979a). The breeding peak of *Actinia equina* coincides with the spring and autumn plankton blooms (Rostron and Rostron 1978) and a similar food availability factor may exist with *Anthopleura* : in summer, newly settled *Hydrococcus* and *Katelysia* juveniles (which have been found in the gut of *Anthopleura*) are abundant below 300 m.

The autumn increase in *Anthopleura* abundance high on the beach may be partly correlated with the increasse in abundance of its preferred hosts, group 2 *Anapella*. There is little change in *Anthopleura* abundance low on the beach in that season, suggesting the high-beach recruitment is not due to an up-beach migration. The large size of the high-beach *Anthopleura* in summer indicates a period of rapid growth there and both this and the increase in abundance could largely be attributed to the autumn recruitment of *Zeacumantus* juveniles (which have been observed in the gut of *Anthopleura*) in that zone.

In general, the size and structure of the *Anthopleura* population at Pipe Clay Lagoon is quite stable. This appears to be characteristic of intertidal anenomes. Batchelder and Gonor (1981), for example, detected no fluctuations in *Anthopleura xanthogrammica*

density over a 2 year period. Also, *Actinia tenebrosa* (adult) populations may vary by less than 3 percent over 3 years (Ottaway 1979a).

Recruitment of anenomes in the rocky intertidal zone is often irregular and locally patchy. Sebens (1982a) detected a massive settlement of *Anthopleura elegantissima* followed by no settlement over the next 4 years. The irregular recruitment in rocky intertidal areas may account for the apparent stability of those populations. In Pipe Clay Lagoon the comparatively homogeneous substrate and sheltered conditions would make *Anthopleura* settlement more regular and the observed changes in population density probably represent annual occurrences. Like other anenome populations, however, the density of adult *Anthopleura* appears to be very stable.

CHAPTER 4

SEASONAL AND SPATIAL VARIATION IN COMMUNITY STRUCTURE

4.1 Introduction

An important concept in the study of community structure is Hutchinson's (1957) n-dimensional hypervolume niche model. According to this model, every organism has a fundamental niche, identifiable as a hypervolume within a n-dimensional coordinate frame, where there are n factors determining an individual's survival. The competitive exclusion principle (Gause 1934; Hutchinson 1959) argues that, in a resource-limited environment, only one species can occupy a fundamental niche. Pielou (1975) pointed out that the appropriate entity to associate with fundamental niches is the gamodene (an interbreeding population of organisms), rather than the species. The use of the species as the basic entity is often an approximation due to convenience, rather than biological sense. Fortunately, the homogeneity of the Pipe Clay Lagoon tidal flat suggests that each species does represent a gamodene.

Species evolve towards establishing unique niches, and thus towards unique locations of their hypervolumes in the niche hyperspace (Whittaker 1972). An expression of the subdivision of a community's hyperspace can be described in terms of the diversity of the community. In its simplest form, diversity is the number of species represented within the community. More useful diversity measures combine the species number and the evenness with which the individuals of the community are apportioned among those species. Of course, the hypervolume/diversity concept is circular in that the apparent subdivision of the community hyperspace must be derived from empirical measures of diversity. Nevertheless, the hypervolume model and the diversity of a community are arguably among the most important concepts in community ecology.

A diversity index can provide a measure with which different (in both a spatial and a temporal sense) communities can be compared. Pianka (1973, 1974, 1975), for example, examined the changes in diversity of desert lizard communities with respect to the fundamental niche dimensions of time, place and food. The change in diversity of communities distributed along environmental gradients has also received considerable

attention (e.g. Sanders 1968; Whittaker 1972; Diamond 1973; Rex 1973).

Following Whittaker (1972), it is useful to define alpha, beta and gamma diversity. Alpha diversity is essentially the localised diversity of a community in a given area; beta diversity measures the rate of species replacement along an environmental gradient and gamma diversity is the overall diversity. Although the intertidal beach of Pipe Clay Lagoon provides a clear environmental gradient, there is no clear turnover of species down the transect and only alpha diversity will be considered in the present study.

In terms of the hypervolume model, high diversity may result from a greater overall availability of hyperspace and/or smaller hypervolume requirements of the species. The diversity may be further modified by the extent of niche overlap that can be tolerated by the species. Pianka (1978) identified 10 mechanisms that can determine the subdivision of the hyperspace:

1. evolutionary time
2. ecological time
3. climatic stability
4. climatic predictability
5. spatial heterogeneity
6. productivity
7. stability of primary production
8. competition
9. rarefaction (density-independent removal of organisms)

and 10. predation

(see also Connell 1978; Thiery 1982).

There have been numerous attempts to amalgamate these mechanisms into a broad theory that describes the determination of diversity and hence the subdivision of the hyperspace. Two of the most resilient theories are the 'predation hypothesis' (Paine 1966, 1971) and the 'competition hypothesis' (Dobzhansky 1950; Pianka 1966). According to the former, selective predation of dominant competitors allows the maintainance of high diversity by preventing the dominant competitors from monopolising the major resource. The competition hypothesis suggests that high diversity arises in stable environments as a result of competition-maintained niche diversification.

Pianka (1966) argued that the two theories were contradictory in that the predation hypothesis suggested that high diversity resulted from a reduction in competition intensity. Menge and Sutherland (1976), however, considered the two theories to be complementary, rather than contradictory. They predicted that competition will be more

important than predation in communities with few trophic levels but as the number of trophic levels and the number of species in those levels increase, predation will become the most important factor.

Sanders (1968, 1969) also provided an important synthesis, the 'stability-time hypothesis', developed to explain the observed increase in diversity with depth below the continental shelf. Sanders suggested that biological adaptations in unpredictable environments are primarily to the physical environment and the communities are therefore 'physically controlled'; in stable environments, the adaptations are primarily to other organisms and the communities are therefore 'biologically accommodated'. Menge and Sutherland (1976) presented two criticisms of this hypothesis. Firstly, they recognised that organisms are usually physiologically adapted to their environment and should not be stressed by its unpredictability. Secondly, they suggested that in unstable environments, specialised consumers at high trophic levels will be faced with less predictable resources and hence the community will be subjected to less effective control by predation.

Rex (1973) showed that the changes in diversity along an environmental gradient, such as that studied by Sanders (1968), are not necessarily monotonic. He observed gastropod diversity to increase from the continental shelf to the bathyal depths but the diversity then decreased markedly out onto the abyssal plain. These observations could not be explained solely in terms of Sander's stability-time hypothesis. Rather, Rex (1976) suggested that both competition and predation are important in structuring deep benthic communities, with the relative importance of one varying inversely with the other.

Huston (1979) developed the dynamic equilibrium theory of species diversity, and he and Rex (1981) suggested that the parabolic pattern of diversity changes observed by Rex (1973) could be predicted by that theory. According to this theory, communities are assumed to exist in a competitive non-equilibrium that results in a dynamic balance between the frequency of population reduction and the rate of competitive displacement, the latter being a positive function of population growth. High nutrient supplies over the upper slopes allow high population growth rates and hence high replacement rates which lead to a rapid approach to equilibrium that cannot be countered by predation. Although low nutrient supplies probably mean abyssal population growth is slow, relatively low predation rates there may allow the community to approach equilibrium. In both cases, the approach to equilibrium leads to intensified displacement of species by dominant competitors and therefore lowers diversity. Huston (1979) cautioned that his hypothesis deals primarily with the maintainance of diversity, as opposed to the evolutionary origin

of diversity.

The intermediate disturbance hypothesis (e.g. Connell 1978) makes similar predictions to the dynamic equilibrium hypothesis but it assumes population reduction occurs due to factors extrinsic to the community. A community that is subjected to frequent disturbance (e.g. physical disturbance) will consist of only those species capable of quickly reaching maturity. If, on the other hand, disturbance is rare, diversity will be reduced by competitive exclusion. Thus, those areas subjected to intermediate levels of disturbance will have more diverse communities.

While there remains a variety of hypotheses about the control of diversity in communities, most now recognise the importance of predation and competition as the overiding determinants of community structure. This contrasts with earlier work, which emphasised the role of environmental factors. Lewis (1978) considered that the transition from physically orientated studies to studies of biological interactions has a concomitant risk that underlying physical factors are neglected. For a thorough understanding of community organistation it appears that environmental factors must be incorporated, particularly with regard to the role they play in regulating predation and competition (Thiery 1982).

On the Pipe Clay Lagoon tidal flat it is unlikely that predation has a dominant role in structuring the community. Within the defined community itself, there are four carnivores: *Nassarius*, *Agatha*, *Cylichnina* and *Anthopleura*. Of these, *Nassarius* is primarily a scavenger, *Agatha* is uncommon and probably a species-specific ectoparasite, and *Anthopleura* is a passive feeder *Cylichnina* may prey on juvenile molluscs

Other potential predators, outside the defined community, include crabs, flatfish and wading birds. Carnivorous crabs are found over much of the beach but probably obtain most of their molluscan food by scavenging. The predatory pressure of the fish would be strongest in those areas of the beach which are most frequently submerged; feeding by wading birds, on the other hand, would be strongest in areas most frequently exposed. Studies by Crawford (1984), however, suggest that molluscs comprise a negligible portion of the diet of flounder in Pipe Clay Lagoon. Wading birds include pied and sooty oyster catchers, eastern golden plovers, red-capped dotterels, red-necked stints and migratory sandpipers (Thomas 1968; Thomas and Dartnall 1971). These animals are likely to include a range of molluscs in their diet (Thomas and Dartnall 1971; Puttick 1977, 1978) but a number of studies have shown that feeding by birds in sandy environments does not greatly affect prey abundance, in contrast to marked reductions in

muddy environments (Quammen 1982). This suggests that predation by waders is unlikely to be important in structuring the mollusc community.

With predation probably playing a minimal role in the organisation of the community, the principal determinants of community structure are likely to be competition and/or environmental effects. Competition, as expressed in the interactive spatial arrangement of species on the tidal flat, will be examined in later chapters. In the following sections, the changes in population structures, and in the overall community structure along the distribution transects are described.

4.2 Methods

4.2.1 A brief review of diversity indices

While the value of diversity as a unifying measure in community ecology is undoubted, the absence of a generally accepted definition of diversity has hindered comparisons between community studies. Numerous indices of diversity have been proposed, each with its own merits and demerits, and each with an ambiguity of interpretation (see Peet 1974; Pielou 1975).

Edgar (1982) examined the commonly used diversity indices and divided them into 3 categories: those sensitive to species richness (Menhinick 1964; Margalef 1967; Kempton and Taylor 1976), those sensitive to species dominance (Simpson 1949; McIntosh 1967; Berger and Parker 1970; Hurlbert 1971) and those of intermediate sensitivity (Shannon in Shannon and Weaver 1949; Brillouin 1962; Hill 1973).

The diversity indices having intermediate sensitivity share a basis in the Shannon (or Shannon-Wiener) index, H', introduced to ecologists by Margalef (1957) and popularised by MacArthur (1965). The Shannon index is defined by

$$H' = -\Sigma p_i \ln p_i$$

where p_i = the proportion of a community's total abundance belonging to the i^{th} species.

Pielou (1975) cautions that H' is applicable only to 'large' communities where the sample is negligible with respect to the remaining community.

In fully censured communities the index of Brillouin (1962) is appropriate:

$$H = N^{-1} \ln [N!/(\pi S_i!)]$$

where N = the total number of individuals in the community

and S_i = the number of individuals in the i^{th} species.

Hill (1973) modified the Shannon index and included the modified form, N_1, in a series N, N_0, N_1, N_2 where

N_0 = the number of species

$N_1 = \exp(H')$

and $N_2 = 1/\Sigma p_i^2$.

The antilogarithmic form of H' replaces the basic unit of H' (which involves a logarithm) by the unit of species; each term in the Hill series then has identical units and their values can be compared in the form of ratios (Hill 1973). The direct relationship

of N_1 to species number also makes the index more readily interpretable (Alatalo and Alatalo 1977). Taille (1979) showed that the Hill ratios are among the most suitable set of parametric families of indices whose members have a varying sensitivity to rare and abundant species.

The terms N_0, N_1 and N_2 may be considered to be the number of all species, the number of 'abundant' species and the number of 'very abundant' species respectively (Alatalo 1981).

The diversity of a community depends on both the number of species and the eveness with which the individuals are divided among them (Pielou 1975). Ideally, measures of eveness should be independent of species number, N_0, (Engen 1979) but the most commonly used measure of eveness,

$J' = H'/\ln N_0$ (Pielou 1966),

is positively correlated with the species number (de Benedictis 1973).

Because the terms of the Hill series have unequal sensitivity to changes in the importance of rare and abundant species, variations in the relative contributions of those species are reflected by variations in the ratios of the terms N_0, N_1 and N_2 (Peet 1974).

The ratio N_2/N_1, originally proposed by Hill (1973) as a measure of eveness has been criticised by Peet (1974) on two grounds. Firstly, a low ratio could either mean that the overall heterogeneity of the community is low or, alternatively, that the dominance is spread over several common species. Secondly, dominance diversity curves (which show index changes resulting from given changes in the importance of species) having slopes approaching zero or infinity will have ratios approaching one.

Alatalo (1981) suggested a modification to the Hill ratio that involves subtracting the minimum that N_1 and N_2 can take (=1 in both cases) from each term in the ratio. The resultant index,

$E = (N_2 - 1)/(N_1 - 1)$,

was shown by simulation studies to overcome the objections of Peet (1974) and appears to be the least ambiguous eveness index (Alatalo 1981).

The indices N, N_0, N_1, N_2 and E are considered to be the most useful measures with which to characterise the changes in the mollusc assemblages in the Pipe Clay Lagoon transects. They are appropriate when the basic unit is 'species', with all size classes pooled to give a total abundance for each species. The same measures can also be used to

show the within-species changes in diversity and evenness; in that case the basic unit is 'size class'.

It is also useful to examine changes in overall diversity and evenness, when the basic unit is 'size class', but all species are included. The above indices are not suitable because they assume that all individuals assigned to the basic unit groups are equal. This is somewhat unrealistic with 'species' as the fundamental unit, but with 'size class' units the realism is highly suspect. Also, the hierarchical categorisation of species and size classes is not accounted for by the usual measures of diversity.

Preston (1969) has described the problems of assigning equal functional roles to different life history stages and Greenberg (1956), Lieberson (1964) and Hendrickson and Ehrlich (1971) have suggested weighting schemes to allow for functional variation. Similarly, all basic unit groupings are assumed to be equally different and weighting schemes (e.g. Lloyd 1964) have been developed to overcome failings of this requirement. In both cases the weighting schemes typically require a measure of the degree of resemblance between classes. This is generally not possible without *a priori* information.

Pielou (1967, 1975) describes methods for dividing the Shannon diversity index into hierarchical components. With 2 levels of categorisation, such as species and size classes, the diversity for the whole community, say H*, is a combination of the species diversity of the community, H'_S, and the mean within-species diversity, H'_C, averaged over all species.

If

q_i = the proportion of individuals of the community that belong to the i^{th} species

and p_{ij} = the proportion of individuals of the i^{th} species that belong to size class j of that species,

then

$q_i p_{ij}$ = the species i, class j abundance expressed as a proportion of the total community abundance,

and

$$H^* = -\sum_{i=1}^{N_0^*} \sum_{j=1}^{s_i} (q_i p_{ij}) \ln (q_i p_{ij})$$

$$= -\sum_i q_i \ln q_i \left(\sum_j p_{ij}\right) + \sum_i q_i \left(-\sum_j p_{ij} \ln p_{ij}\right)$$

$$= H'_S + H'_C \qquad \text{(Pielou 1975).}$$

Here N_0^* = the total number of species and s_i = the number of classes in species i.

Applying Hill's (1973) antilogarithmic modification to H* gives

$$\exp(H^*) = \exp(H'_S + H'_C) = \exp(H'_S)\exp(H'_C).$$

Thus,

$$N_1^* = \exp(H^*) = (N_{1S})(N_{1C}).$$

Also,

$$N_2^* = \left[\sum_{i=1}^{N_0^*} \sum_{j=1}^{s_i} (q_i p_{ij})^2 \right]^{-1}$$

and hence

$$E^* = (N_2^* - 1)/(N_1^* - 1).$$

The Hill series and related term equivalents to Pielou's (1967, 1975) hierarchical diversity indices are therefore given by N, N_0^*, N_1^*, N_2^* and E* and these characterise a community when the basic unit is 'size class'. While the methods of hierarchical diversity cannot completely remove the problems of assigning equal functional roles to different life history stages, they do reduce the discrepancies to a minimum, given the absence of *a priori* information.

4.2.2 Analysis of Pipe Clay Lagoon data

Diversity indices were calculated according to the Hill (1973) series. In the following section, the indices are always presented in the sequence N, N_0, N_1, N_2 and E.

Each season's set of 36 distribution transect quadrats allows the serial changes in community structure to be examined. The analysis can be conducted at three levels. Most studies of diversity examine the species diversity of an assemblage where 'species' is the basic unit. This is considered here but the hierarchical and within-species diversity are also included to introduce greater fidelity.

The serial changes in species diversity of the assemblage are presented for each season. To examine the importance of the juvenile animals in determining the apparent diversity, the species diversity, calculated with the exclusion of 0 mm animals is also shown.

With 'size class' as the fundamental unit, the serial changes in the hierarchical diversity for each transect were calculated and are included for comparison with the

simple species diversity.

To examine the within-species diversity patterns, the changes in the relative proportions of the size classes for each species are presented graphically, in the form of three dimensional SURFACE2 plots. These changes are reflected in the changes in the within-species diversity terms.

4.3 Results

4.3.1 Changes in the assemblage structure along the distribution transects

The changes in the relative abundance of the size classes of each species (except *Microdiscula*) along the distributional transects are shown in Figs. 4.1-4.15, in the form of SURFACE2 plots. While the usefulness of these plots is obviously limited in the case of rare species, or those species with few size classes, they do allow a visual identification of the temporal and spatial changes in the structure of the assemblage. The changes will be examined species by species, in the order: bivalves, gastropods and then *Anthopleura* .

4.3.1.1 *Anapella* (Fig. 4.1)

The general trend is for a steady increase in relative abundance from 0 m to 400 m prior to a sharp decrease associated with the 500 m beach ridge. The numbers recover only slightly in the subsequent lower beach slope, indicating a loose correlation between beach height and *Anapella* abundance. There is evidence, however, for an (at least partial) inverse dependence of abundance on beach height. Thus, the major abundance peak is associated with the 400 m beach trough and the numbers decrease with beach height above that zone. There also appears to be a synergistic effect with season. For example, the decrease in numbers above the 300 m ridge is exaggerated in summer while the increase in the beach trough is less pronounced in that season.

The 0 mm size class shows relatively constant representation from 60 m to 480 m, where there is a decrease associated with the beach ridge at 500 m, followed by a slight increase below the ridge. The 1 mm and 2 mm classes follow similar patterns to the 0 mm animals although they exhibit more fluctuations in abundance. These 3 classes form a distinct group in each season's plot.

A second group is formed by animals larger than 10 mm, and these cluster in the plots between 40 m and 500 m, with peak abundances occurring close to 200 m.

The winter (270681) plot shows a third, intermediate size group lying between 40 m and 400 m. This group is less distinct in other seasons but is always represented.

4.3.1.2 *Katelysia* (Fig. 4.2)

The plots for *Katelysia* are approximately mutually exclusive to those for *Anapella* . A superposition of each season's plot for the two species shows an interlocking pattern that approximately fills the whole area of the resultant plot.

Like those of *Anapella* , the *Katelysia* populations are characterised by relatively large proportions of juvenile (0 mm) animals. *Katelysia* is restricted to below 300 m and numbers increase between that distance and 700 m, interrupted by the 500 m beach

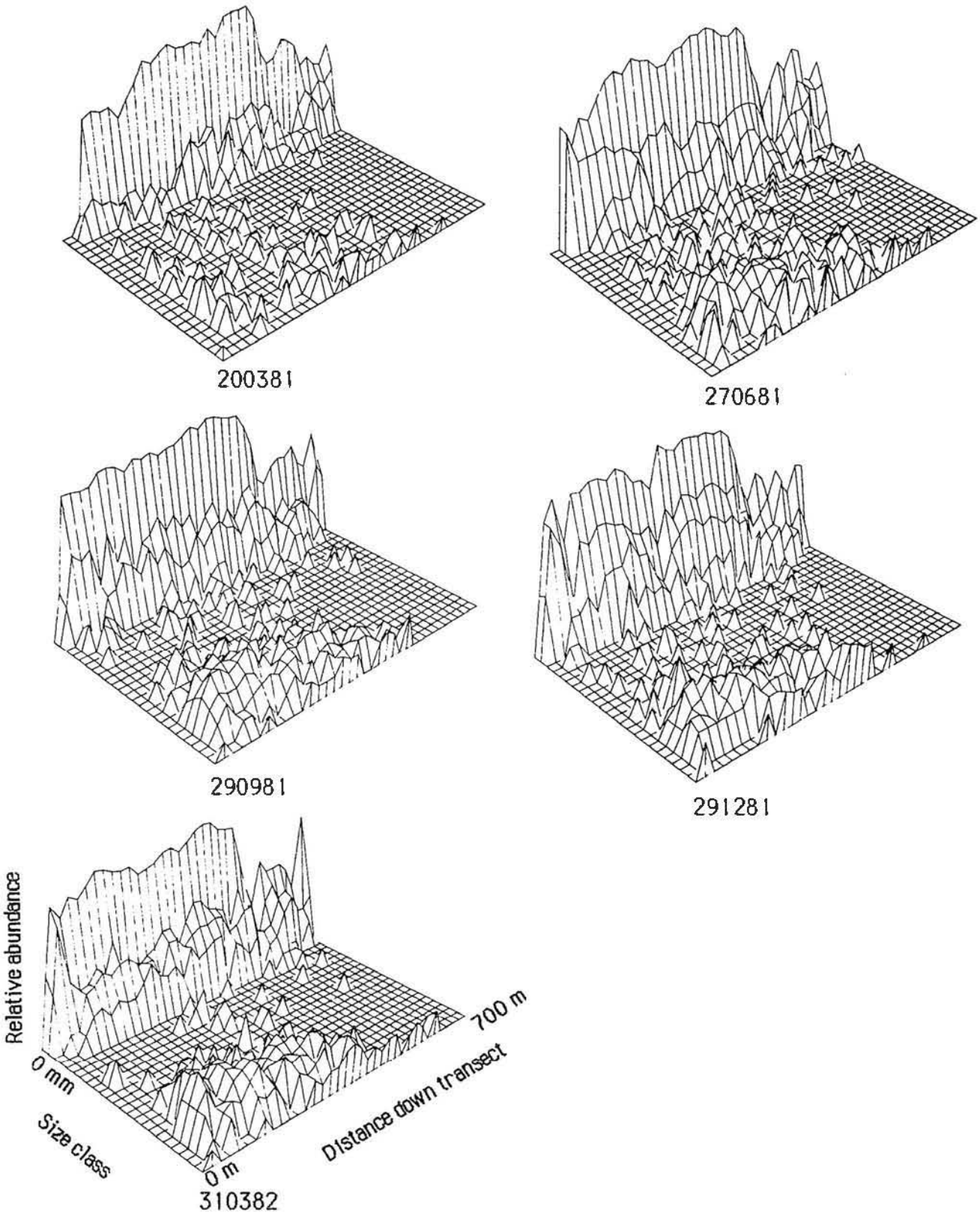


Fig. 4.1 Changes in the relative abundance of *Anapella* size classes along the distribution transects. Abundances are logarithmic and are expressed as a proportion of the maximum abundance. Size class intervals are 1 mm; transect intervals are 20 m.

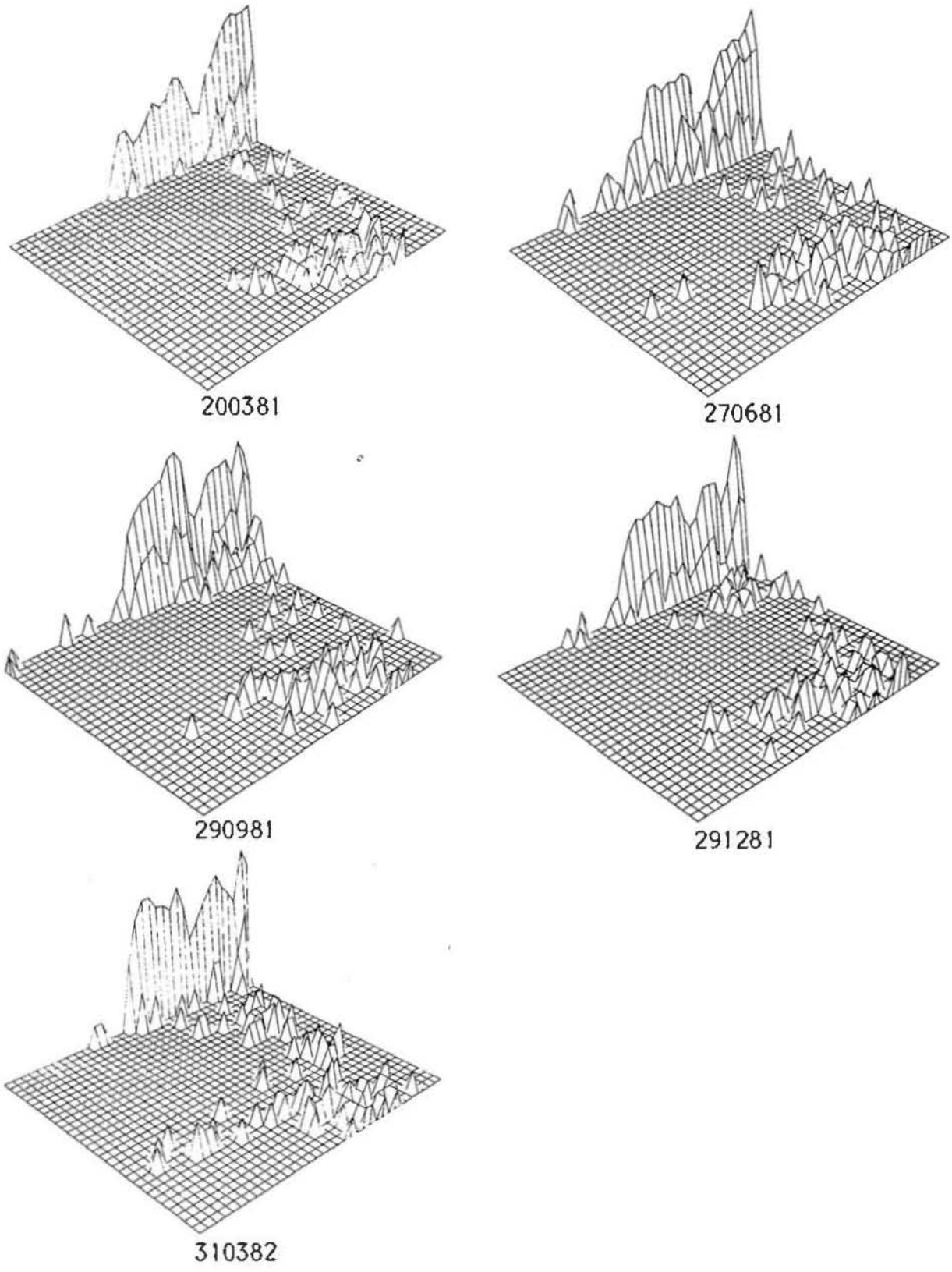


Fig. 4.2 Changes in the relative abundance of *Katelysia* size classes along the distribution transects. Axes as in Fig. 4.1.

ridge which produces a trough in abundances.

The relative seasonal differences in overall abundance differ either side of the beach ridge. On the upper side of the ridge, the spring abundances are markedly higher and the 200381 autumn and the winter numbers are slightly lower than the summer and 310382 autumn values. Below the ridge the 200381 autumn and the summer numbers are considerably greater than those of the other seasons.

The 0 mm and 1 mm classes of *Katelysia* both have a general increase in abundance from about 300 m to 700 m with a drop in numbers over the ridge centered at 500 m.

A second major group is formed by animals larger than 20 mm which are found predominantly between 300 m and 600 m.

A third, intermediate size group of 3 mm to 10 mm animals lies below 500 m and is most distinct in summer (291281).

4.3.1.3 *Wallucina* (Fig. 4.3)

Wallucina is never abundant in the distribution transects and is largely restricted to below 300 m. In spring a well defined peak lies between about 350 m and 450 m. There is no evidence that the size classes have different distributions along the transects.

4.3.1.4 *Soletellina* (Fig.4.4)

The *Soletellina* populations show more structure along the distribution transects than do those of *Wallucina*. Numbers are low in autumn (200381 and 310382) but increase through winter to summer. The animals are generally restricted to below 400 m and are most abundant below 600 m. There is representation of the smaller size classes further up the beach in spring but this is less marked in other seasons.

The populations become more structured in summer as the juveniles of the previous seasons grow.

4.3.1.5 *Hydrococcus* (Fig.4.5)

Three main features can be identified in the overall abundance pattern. The first is a broad peak between 0 m and 200 m, centred close to 100 m. This is followed by a smaller peak between 250 m and 300 m. Below 500 m the abundances increase greatly. The relative seasonal positions of the abundance curves are basically similar in each of these areas, the differences being exaggerated with increased abundance. Comparatively low numbers in autumn (200381) and winter give way to an increase over spring to reach a maximum in summer prior to a decline to the following autumn.

The patterns for the different size classes are basically similar but the 0 mm class shows exaggerated changes relative to the other classes. Also, the patterns for each season are similar.

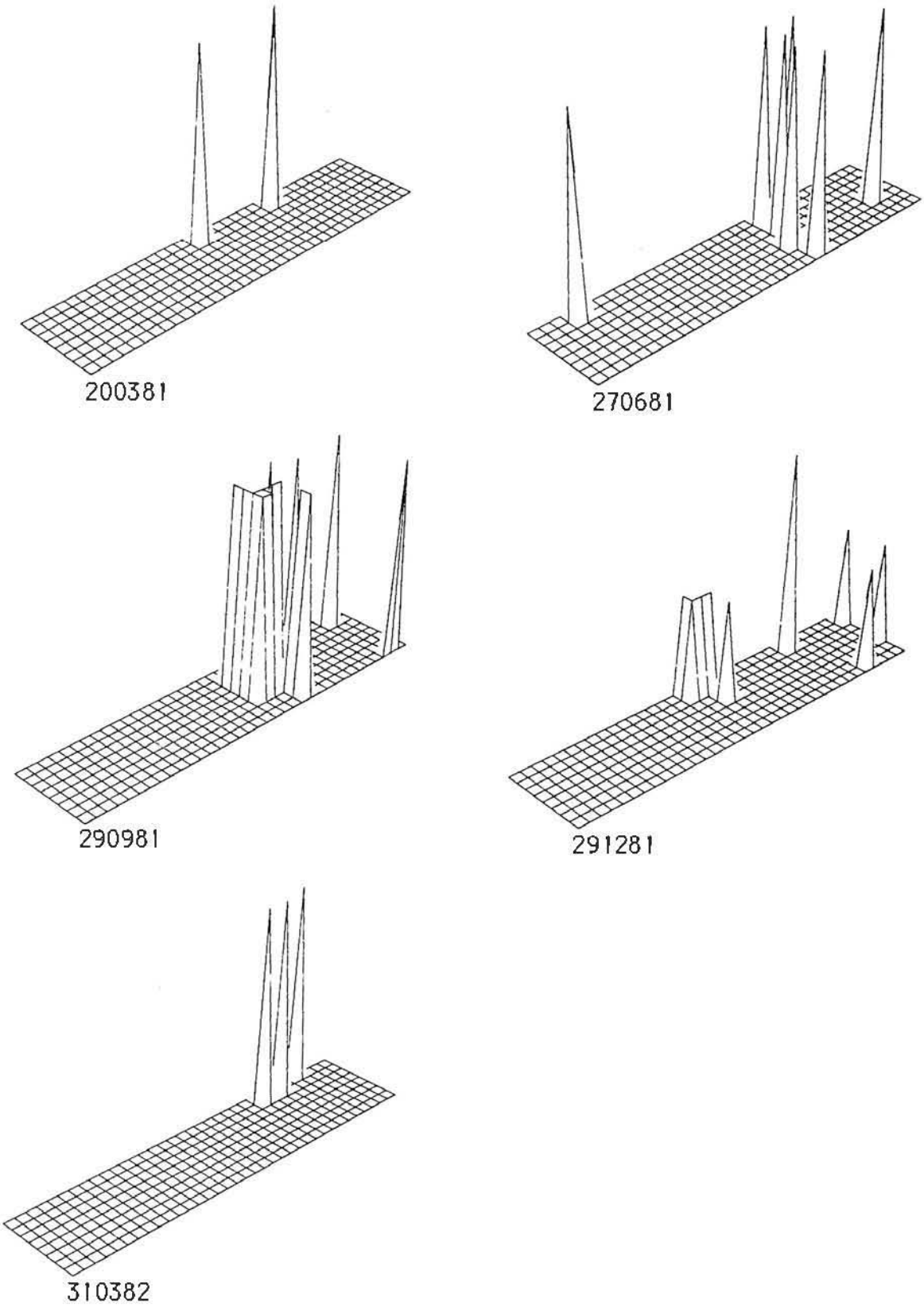


Fig. 4.3 Changes in the relative abundance of *Wallucina* size classes along the distribution transects. Axes as in Fig. 4.1 except that abundances are not logged.

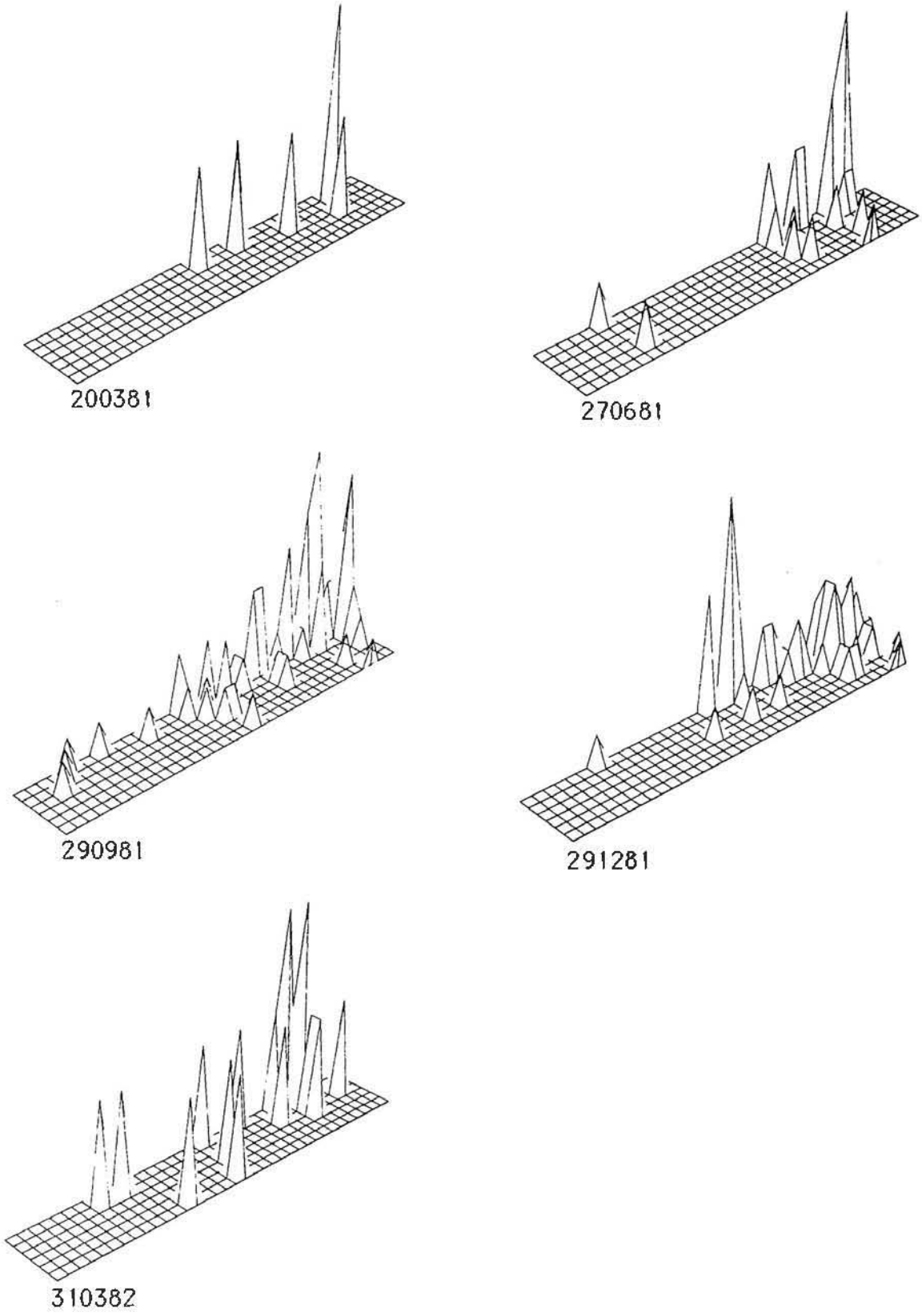


Fig. 4.4 Changes in the relative abundance of *Soletellina* size classes along the distribution transects. Axes as in Fig. 4.3.

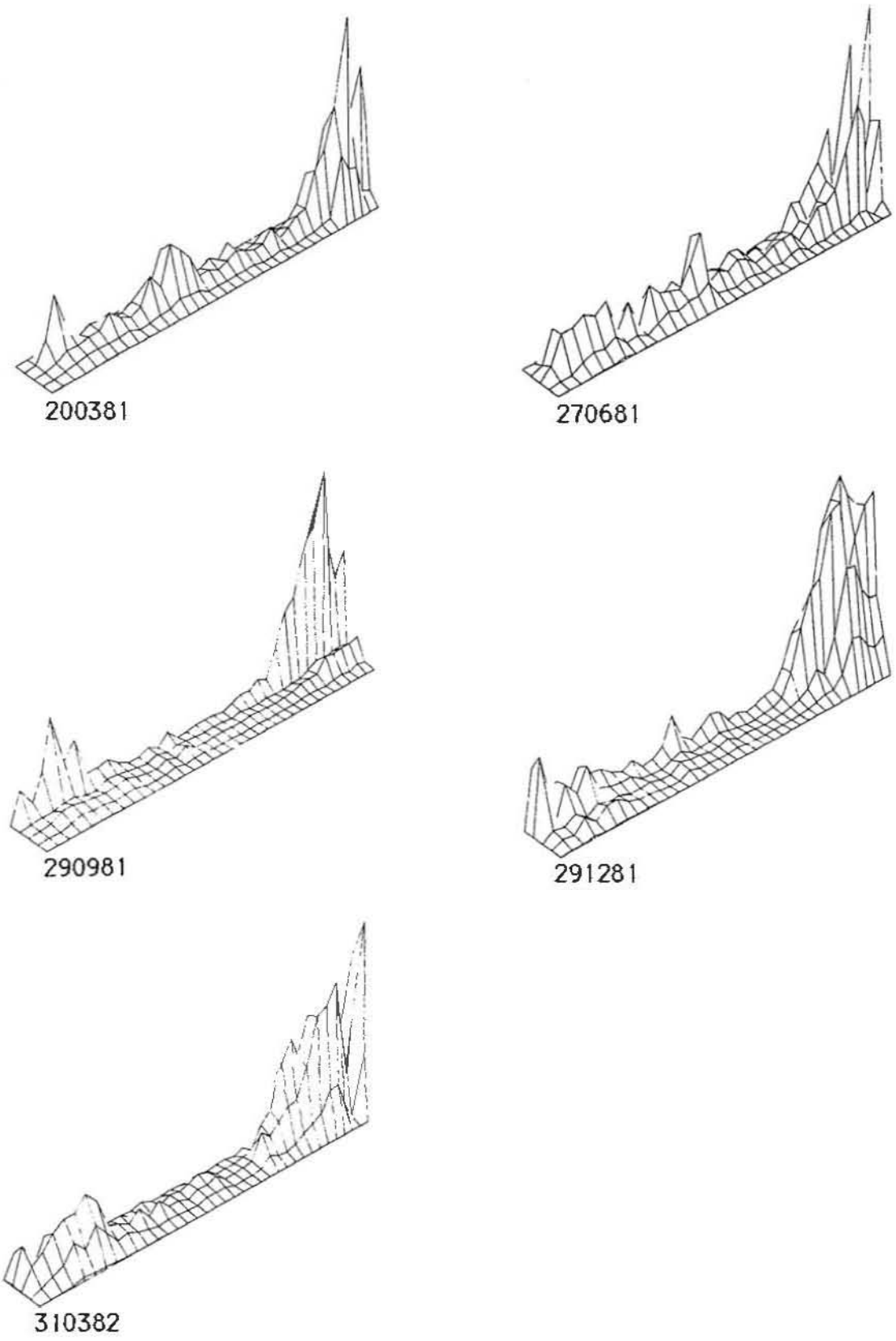


Fig. 4.5 Changes in the relative abundance of *Hydrococcus* size classes along the distribution transects. Axes as in Fig. 4.3.

4.3.1.6 *Zeacumantus* (Fig. 4.6)

In the 200381 autumn, an initial rapid rise to an overall abundance peak near 100 m, followed by a slight decline and then another rapid rise, leads to maximum numbers near 300 m; there is then a sudden drop to 400 m. This pattern is partially retained in winter but the upper beach peak is more pronounced; the 270681 pattern is intermediate between the 230381 and 290981 curves. There is a marked reduction in the significance of the upper beach peak in summer but the peak becomes more defined the following autumn.

The net change in the distribution patterns of *Zeacumantus* appears to be a progressive shifting of the maximum peak up the beach during the sampling period. Most classes show an increase in abundance from 0 m to a peak close to 100 m followed by a gradual decline prior to the 400 m cutoff. The plots also show a general gradient from peak abundances in the small size classes to lower abundances in the larger classes. This is a relatively uniform gradient in most seasons, although in the 200381 autumn there is a comparative excess of 0 mm animals.

4.3.1.7 *Salinator* (Fig. 4.7)

Salinator abundances are comparatively low over the whole beach in autumn and winter. A large increase in overall abundance in spring throughout the transect is followed by a reduction in numbers over the summer and autumn. Three main areas of increase are apparent. The first lies in the extreme upper beach, above 50 m, the second between 100 m and 300 m and the third below 400 m. The latter is the principal area of the spring increase and numbers are highest near 600 m prior to a decline to 700 m.

The first region is characterised by relatively high numbers of large animdals on 200381 and 270681 and high numbers of small animals in the other seasons (including 310382). The second region shows low numbers of small animals on 200381 and 270681 but those animals are well represented in the other seasons. The third region has relatively high numbers of small animals in all seasons.

4.3.1.8 *Cylichnina* (Fig. 4.8)

Three peaks are evident in the abundance curves, but are clearly defined only on 200381. The first lies between 100 m and 250 m, the second between 300 m and 450 m and the third below 500 m; each successive peak is higher. There is also a progressive increase in overall abundance from autumn to summer and a subsequent decrease the following autumn.

The *Cylichnina* populations are comparatively poorly structured on 200381 and 270681. On these dates the proportional representation of size classes is irregular, in

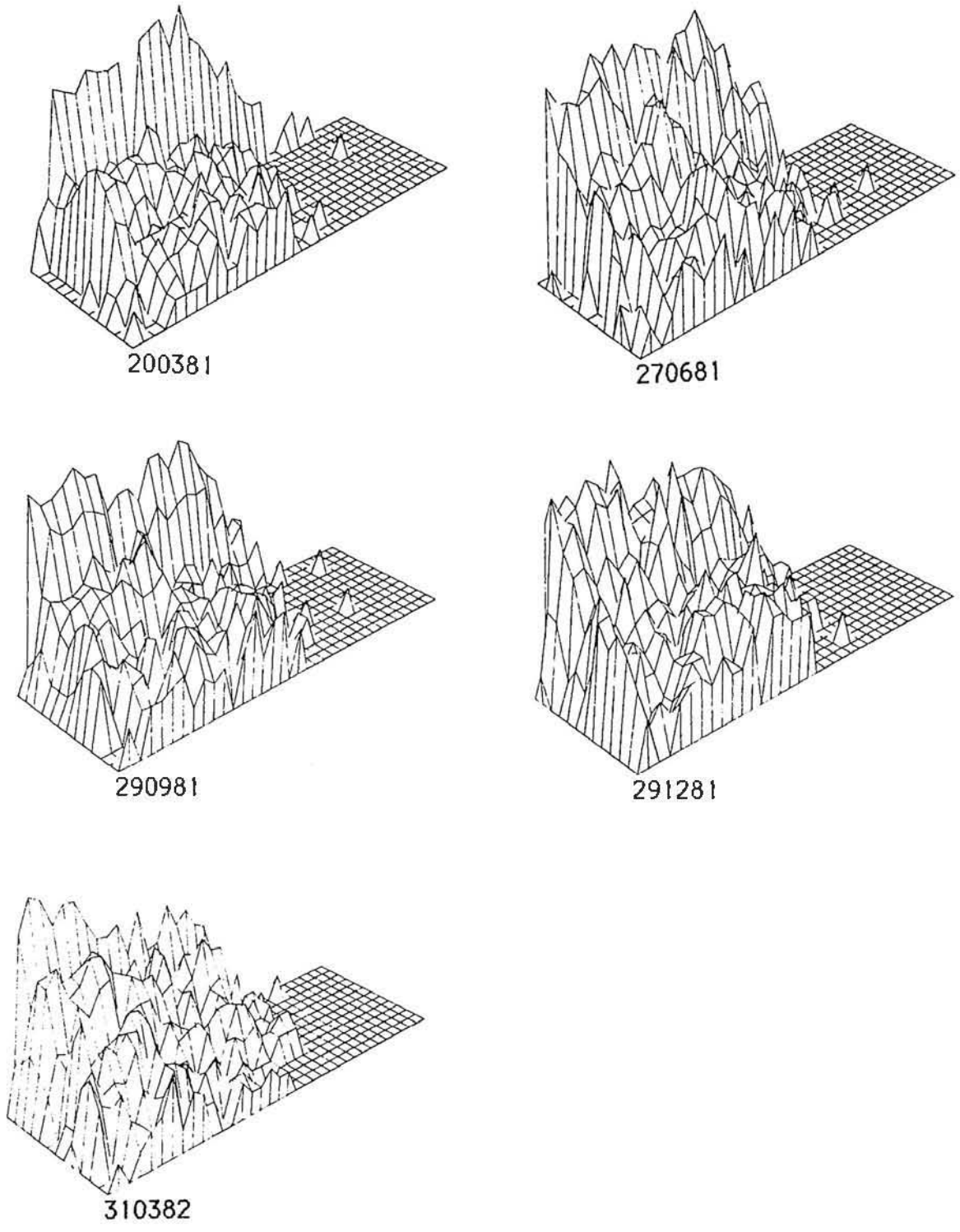


Fig. 4.6 Changes in the relative abundance of *Zeacumantus* size classes along the distribution transects. Axes as in Fig. 4.1.

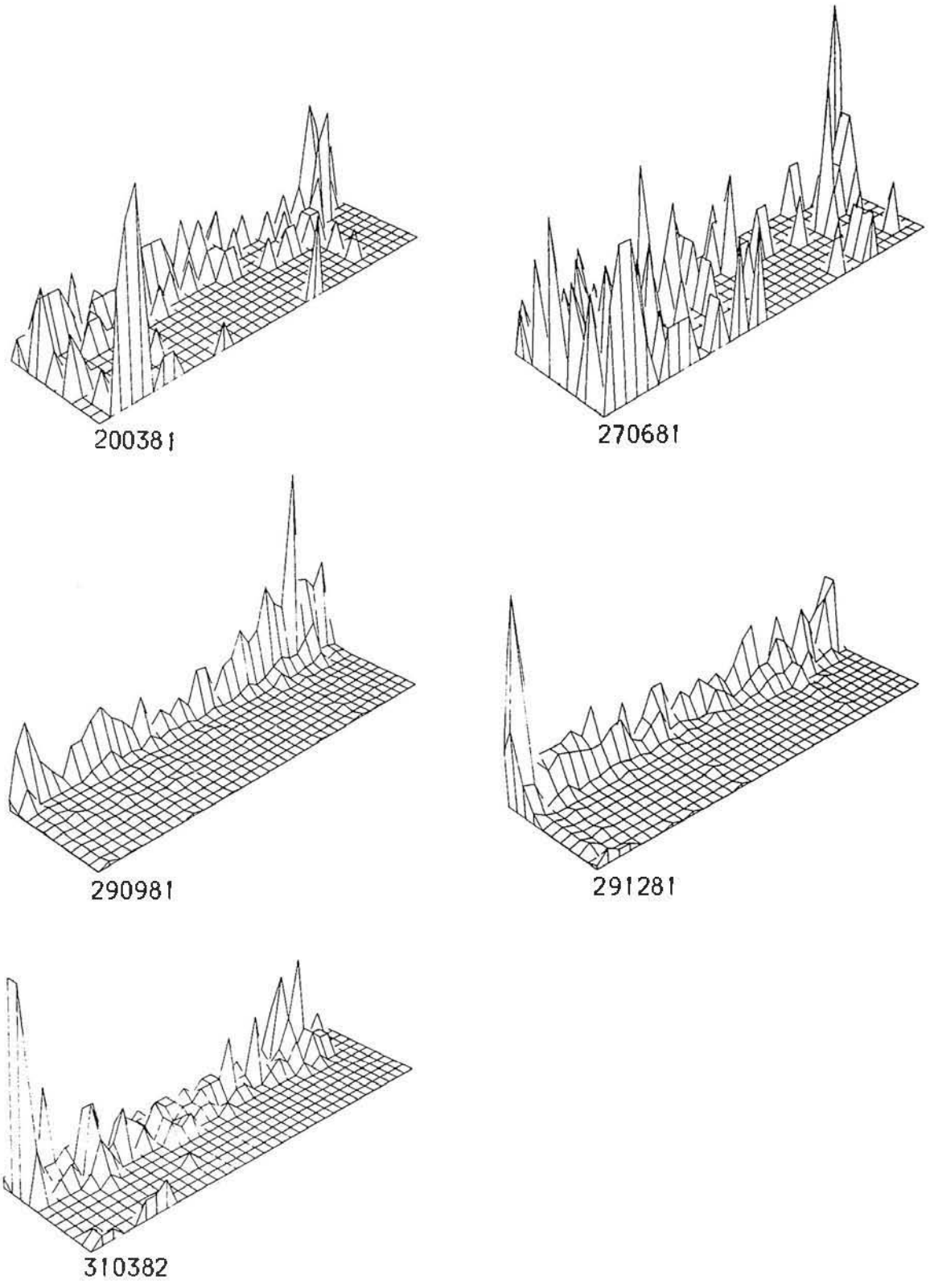


Fig. 4.7 Changes in the relative abundance of *Salinator* size classes along the distribution transects. Axes as in Fig. 4.3.

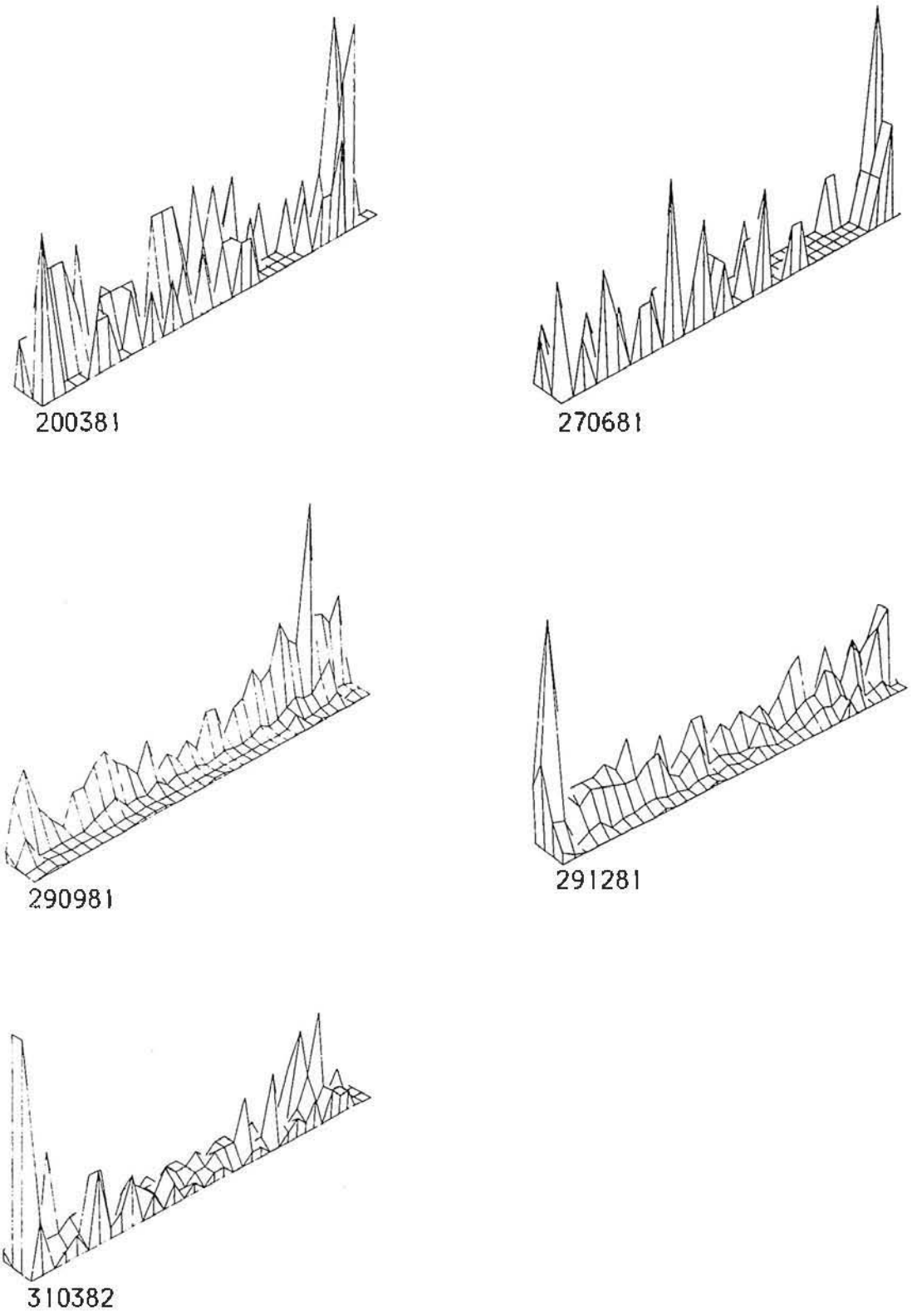


Fig. 4.8 Changes in the relative abundance of *Cylichnina* size classes along the distribution transects. Axes as in Fig. 4.3.

contrast to the fairly constant representation on 290981; there is a decrease in this constancy from 291281 to 310382.

4.3.1.9 *Rissopsis* (Fig. 4.9)

Rissopsis exhibits two areas of high abundance that are seasonally dependent. Between 0 m and 300 m, numbers are high in spring and the 310382 autumn. Below 400 m, the numbers are high in spring only, although in winter there is an abundance peak in the last 50 m of the beach. Like *Cylichnina*, the *Rissopsis* populations are poorly structured on 200381 and 270681. On 290981, three distinct regions of abundance can be identified; these may have begun to emerge over winter. The principal region lies between 0 m and 300 m with secondary and tertiary regions below 600 m and near 500 m respectively. All but the principal region disappear through 291281 and 310382. There is a marked difference between the 200381 and 310382 autumn patterns.

4.3.1.10 *Microdiscula*

There are no well defined seasonal trends and *Microdiscula* is restricted to between 50 m and 400 m. Numbers are always low.

4.3.1.11 *Nassarius* (Fig. 4.10)

There are no clear trends in the abundances of *Nassarius* although there is a poorly defined peak between 100 m and 400 m. Numbers are low in all seasons.

In contrast to most of the other species of gastropods, *Nassarius* is poorly represented in the small size classes. The great majority of animals are greater than 10 mm in size. Only in summer and the 310382 autumn are juveniles found in significant numbers (below 500 m). Overall, the *Nassarius* populations are poorly structured.

4.3.1.12 *Agatha* (Fig. 4.11)

Agatha is found principally between 100 m and 400 m but is only consistently abundant in winter, when numbers increase sharply near 100 m before gradually declining.

Agatha also shows little structuring of its populations along the distribution transects. Animals occur principally between 100 m and 400 m but only on 270681 is this region clearly defined. Although the numbers are low, there appears to be no difference in distributions between the various size classes.

4.3.1.13 *Bembicium* (Fig. 4.12)

Bembicium is generally restricted to the first 100 m of the beach although individuals are irregularly scattered further down the beach. The population structures

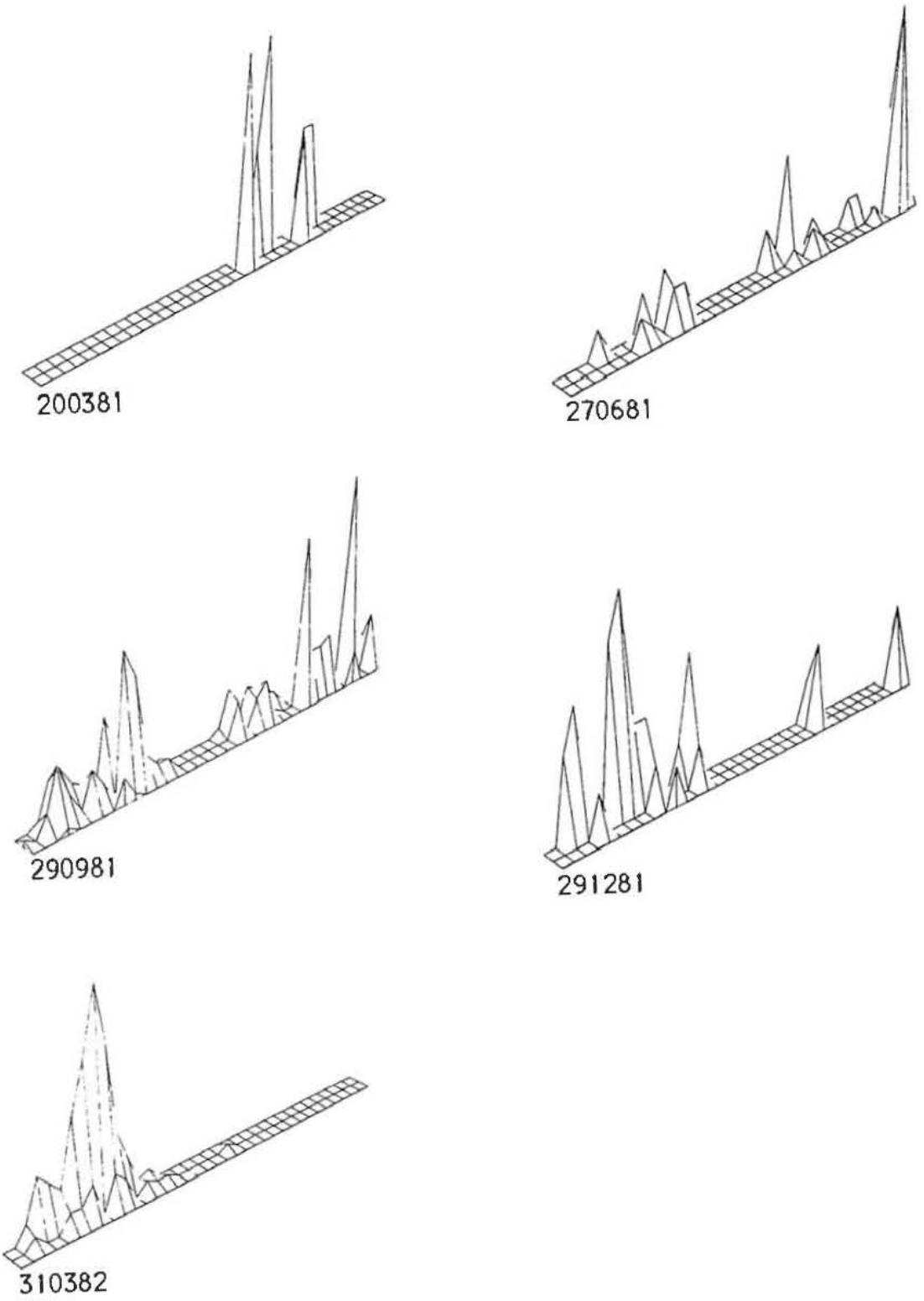


Fig. 4.9 Changes in the relative abundance of *Rissopsis* size classes along the distribution transects. Axes as in Fig. 4.3.

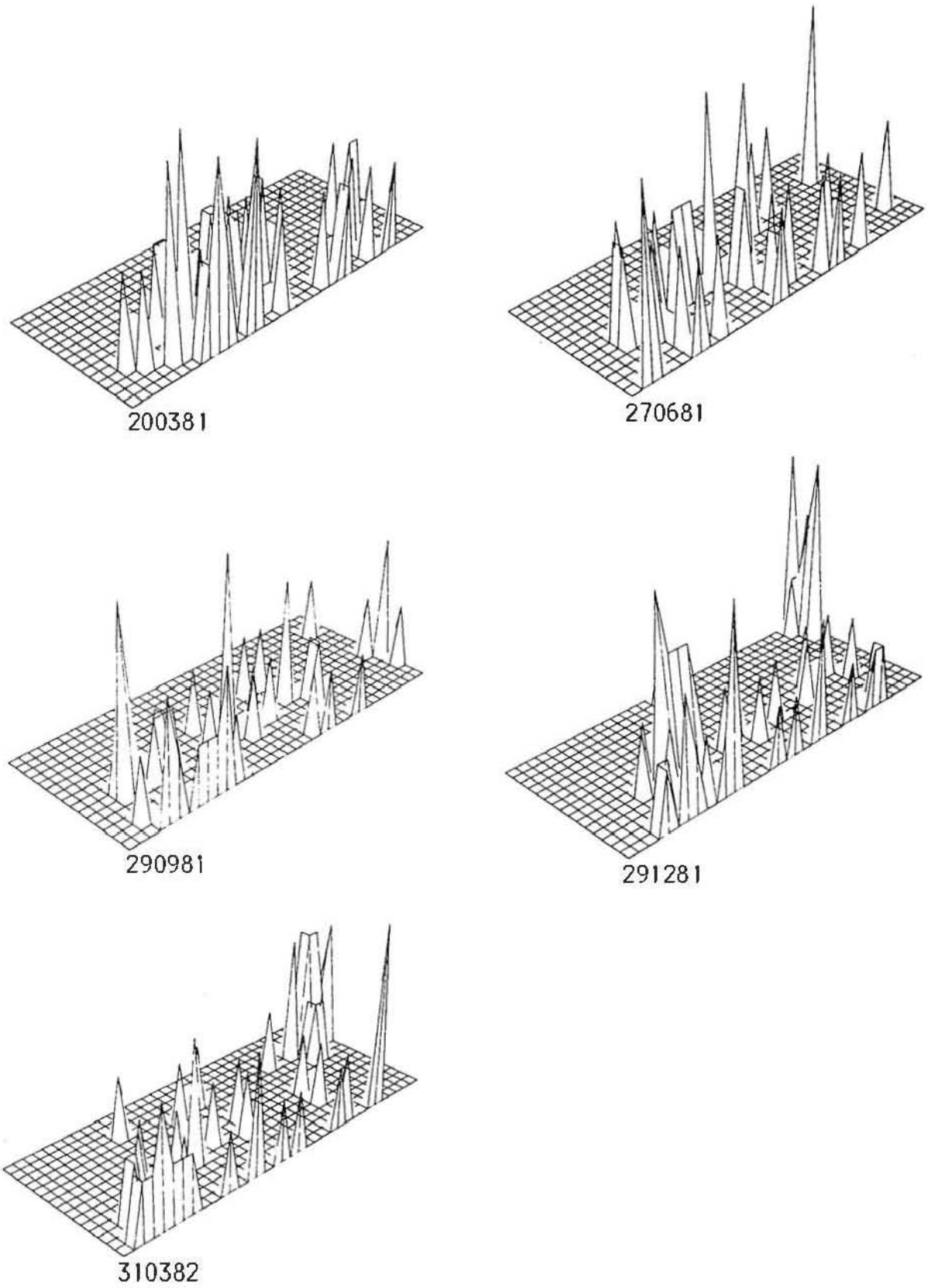


Fig. 4.10 Changes in the relative abundance of *Nassarius* size classes along the distribution transects. Axes as in Fig. 4.3.

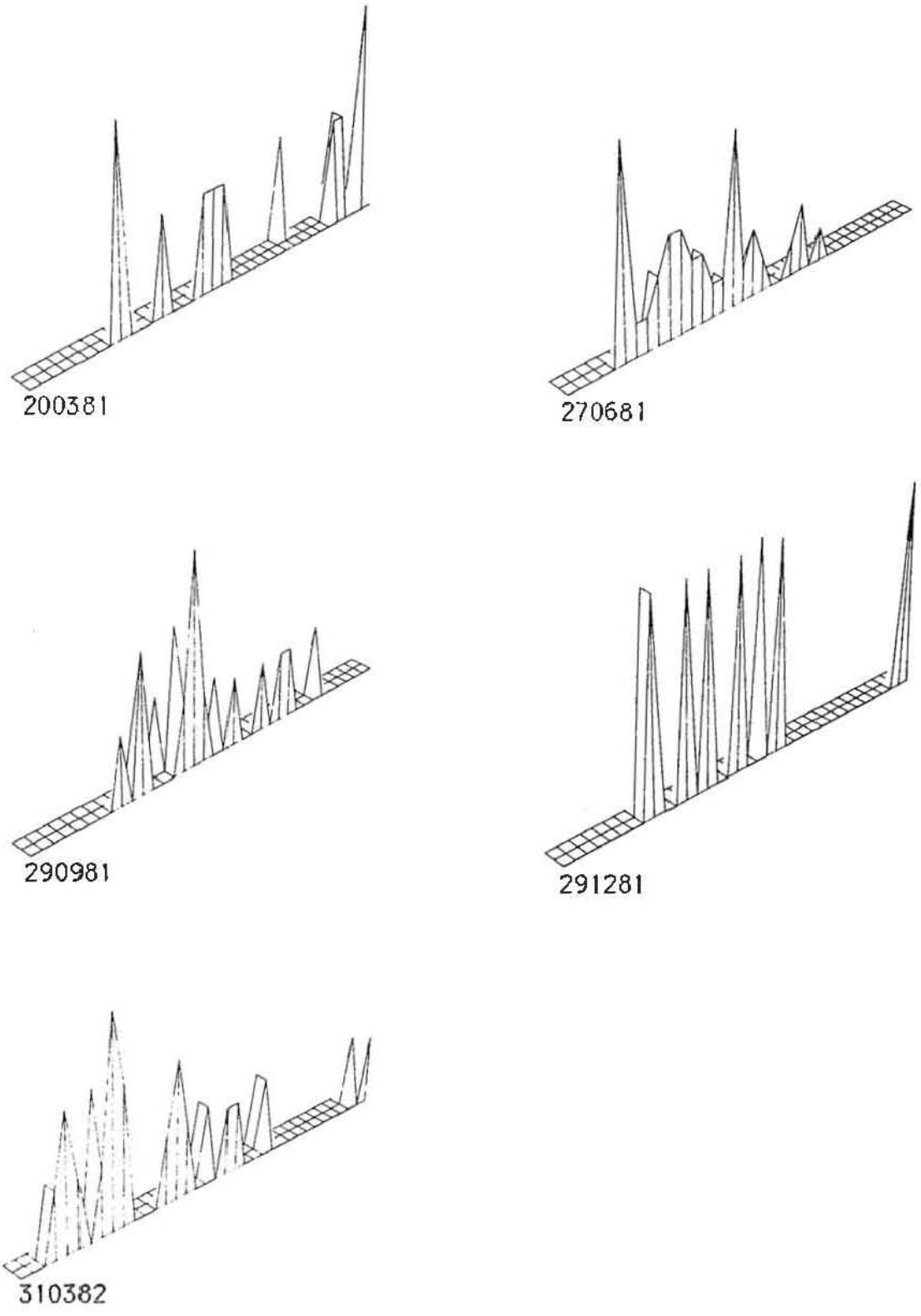


Fig. 4.11 Changes in the relative abundance of *Agatha* size classes along the distribution transects. Axes as in Fig. 4.3.

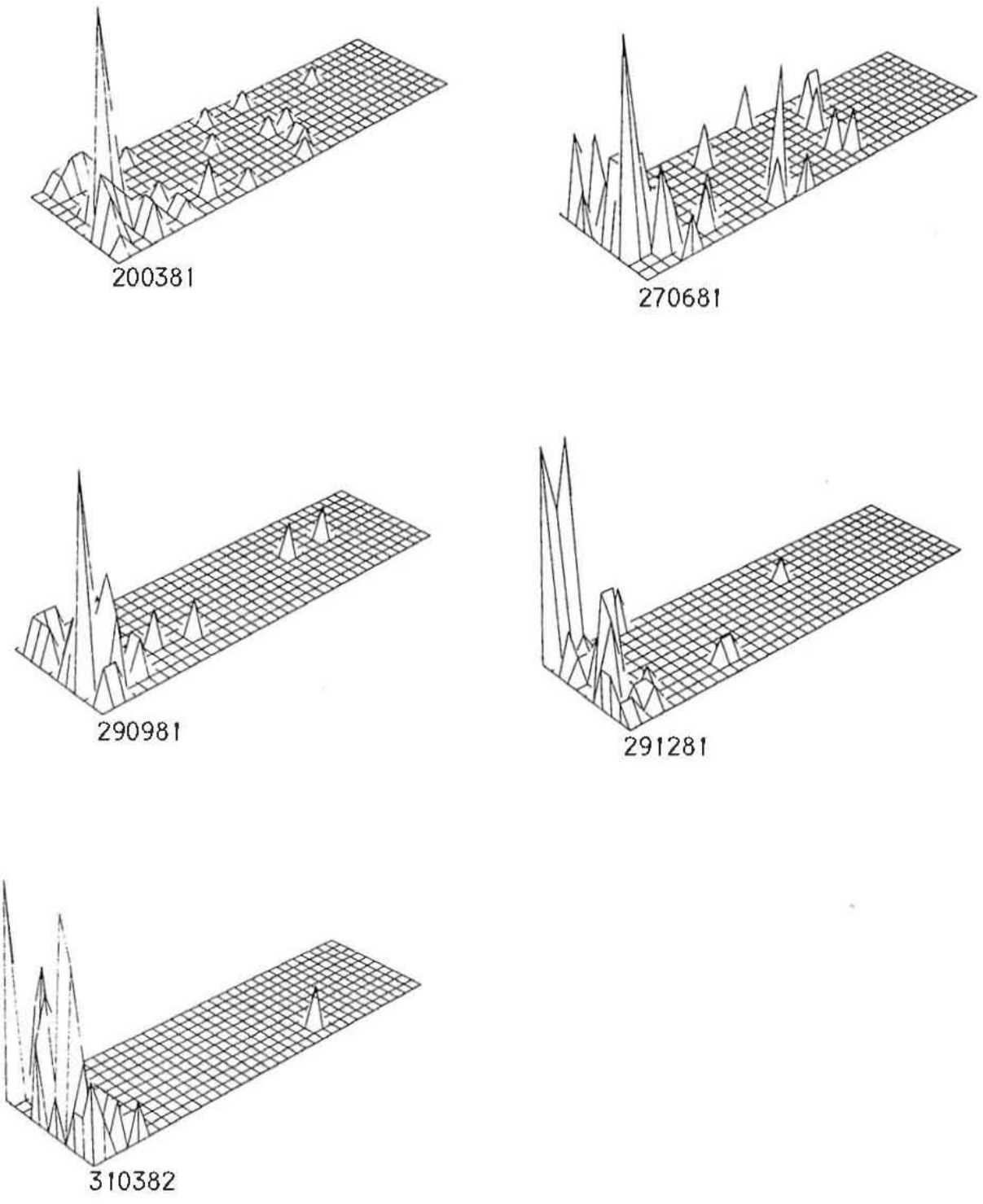


Fig. 4.12 Changes in the relative abundance of *Bembicium* size classes along the distribution transects. Axes as in Fig. 4.3.

are fundamentally similar between 200381 and 290981 but on 291281, and to a lesser extent 310381, there is a relative increase in the number of juveniles. In all seasons, a primary feature of the plots is the abundance peak of 5 mm to 10 mm animals between 0 m and 60 m.

4.3.1.14 *Austrocochlea* (Fig. 4.13)

The plots for *Austrocochlea* show poorly structured populations grossly similar to those of *Nassarius*. Juveniles are scarce and the majority of individuals are found between 500 m and 700 m.

4.3.1.15 *Notoacmea* (Fig. 4.14)

Notoacmea exhibits plots basically similar to those of *Austrocochlea* in that the majority of animals are large and found between about 500 m and 700 m. The apparent absence of detailed structure within the populations may, in part, be due to the choice of 5 mm being the accumulating size class (i.e. animals larger than 5 mm are included in the 5 mm class); a larger size for the accumulating class may have been more suitable.

4.3.1.16 *Anthopleura* (Fig. 4.15)

In general, total *Anthopleura* abundances increase steadily from 50 m to near 500 m before a rapid decline. Numbers remain low between 500 m and 700 m. Minor, poorly defined peaks occur between 100 m and 200 m and 300 m and 400 m. The pattern, in fact, is very similar to that of *Anapella*; with *Anthopleura*, however, the abundance curves are not dominated by juveniles.

Overall numbers are lowest on 200381 but increase over the following seasons. The 310382 autumn numbers are considerably higher than those of the previous autumn. There are seasonal changes in the strength of the structuring although the basic pattern remains the same. There is a trend for increasing structure from 200381 through to 291281 followed by a decrease the following (310382) autumn. The size class representation is approximately symmetrical about the median size, 5 mm.

4.3.2 Changes in the Hill terms along the distribution transects

The changes in the Hill terms for species diversity, with and without 0 mm animals, are shown in Figs. 4.16 and 4.17 respectively. The hierarchical diversity changes are shown in Fig. 4.18. The within- species diversity patterns were non-trivial for the two most abundant bivalves (*Anapella* and *Katelysia*), the three most abundant gastropods (*Hydrococcus*, *Zeacumantus* and *Salinator*) and the anenome, *Anthopleura*; plots of the changes in the Hill ratio terms are given (Figs 4.19 through 4.24).

For convenience, the diversity, heterogeneity and evenness coefficients will be refered to under the collective term 'diversity coefficients'.

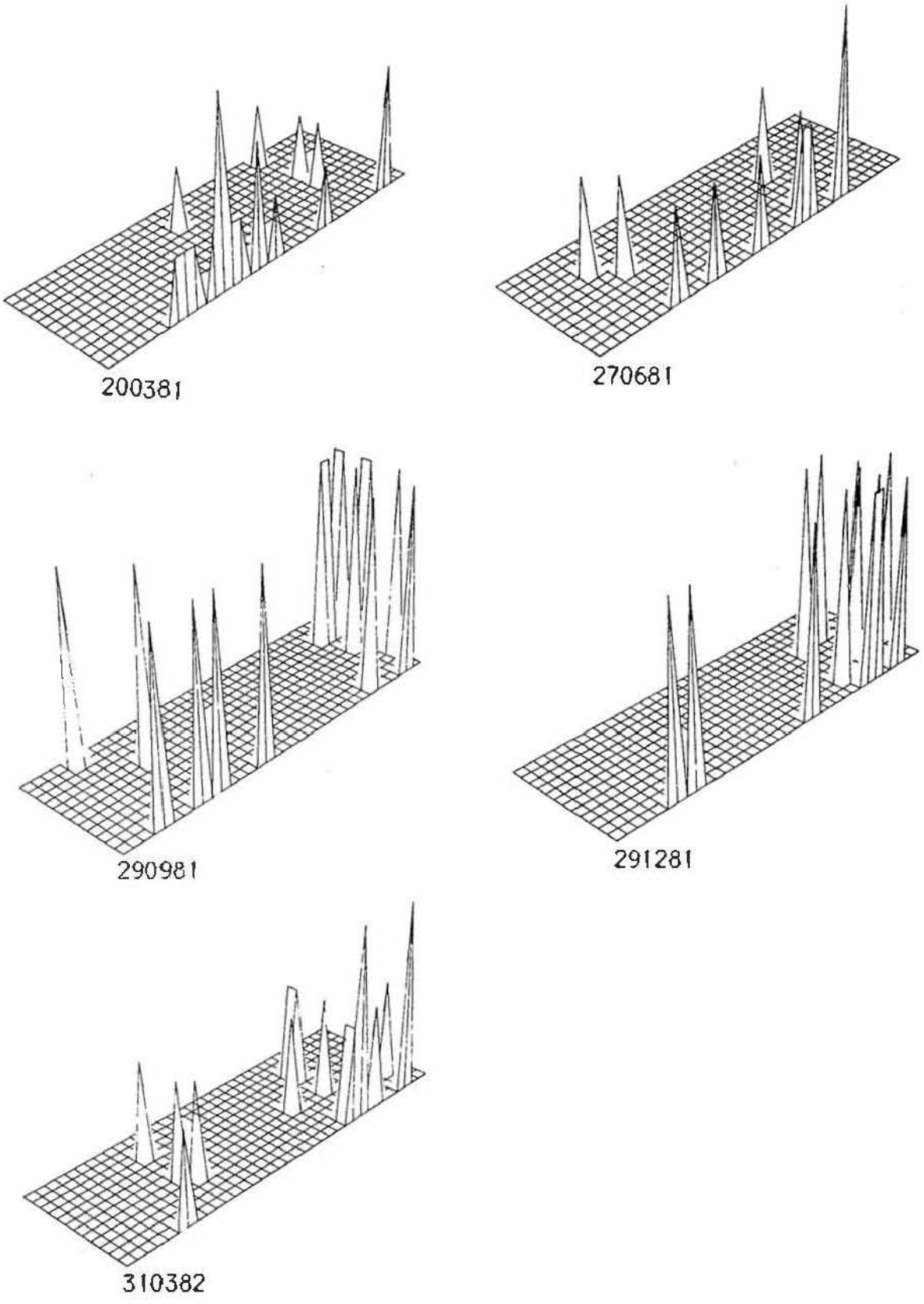


Fig. 4.13 Changes in the relative abundance of *Austrocochlea* size classes along the distribution transects. Axes as in Fig. 4.3.

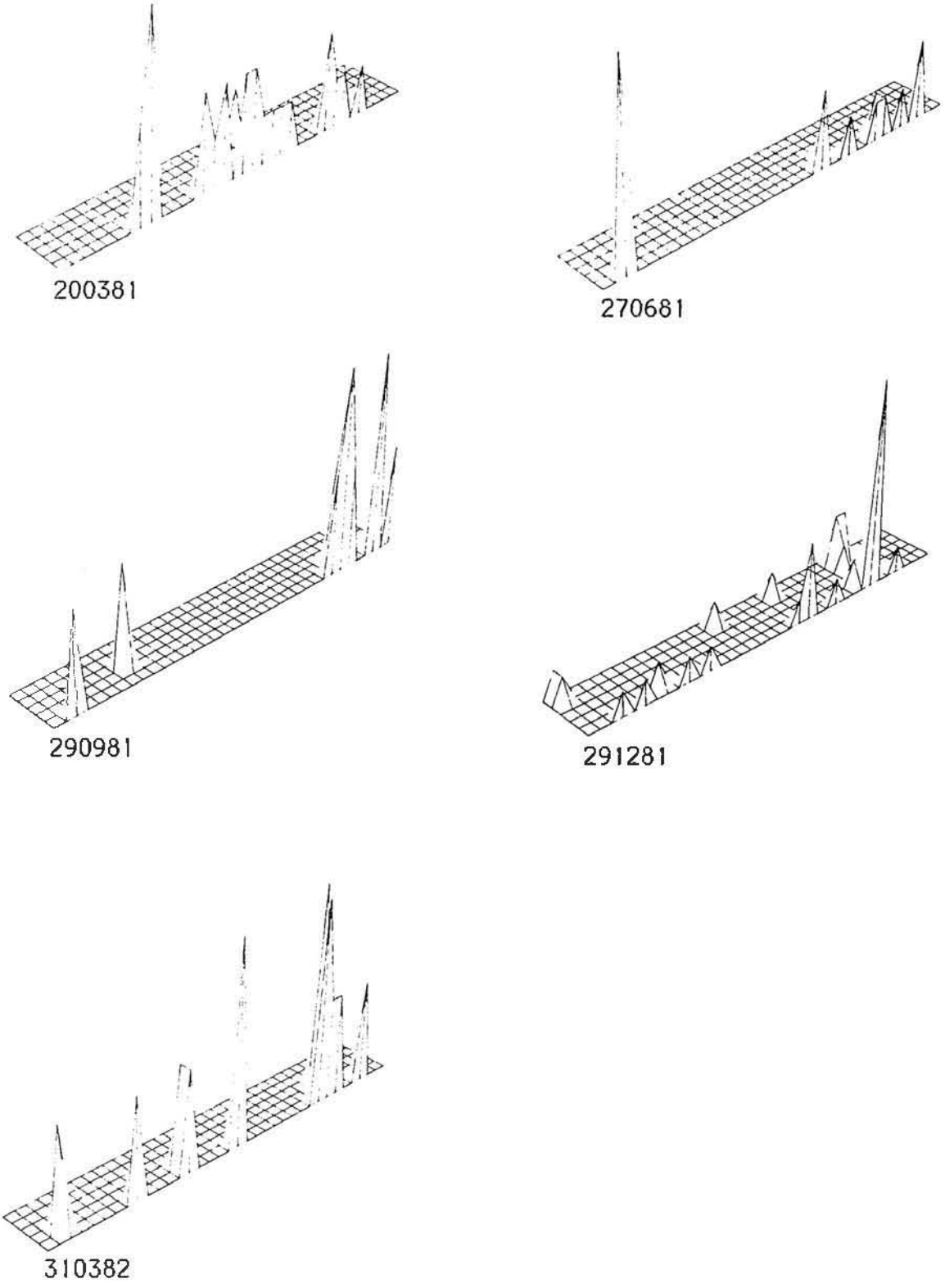


Fig. 4.14 Changes in the relative abundance of *Notoacmea* size classes along the distribution transects. Axes as in Fig. 4.3.

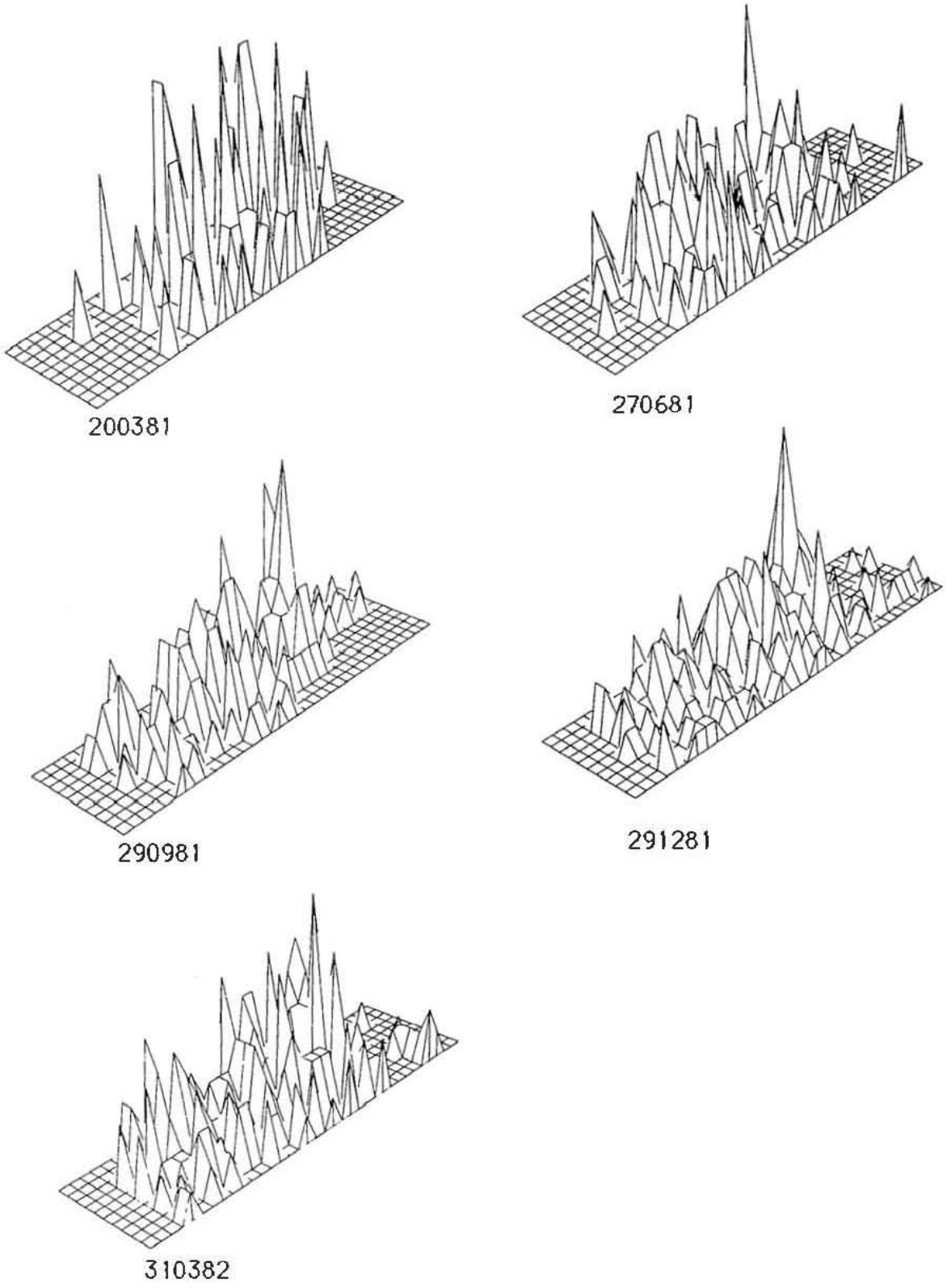


Fig. 4.15 Changes in the relative abundance of *Anthopleura* size classes along the distribution transects. Axes as in Fig. 4.3.

4.3.2.1 Species diversity (Fig. 4.16)

Overall community abundance (Fig. 4.16(a))

Five principal features can be recognised in the plot of the seasonal changes in the overall community abundance, although each season shows departures from the general trend. In general, there is a rapid rise in abundance during the first 50 m of the beach, reaching a broad peak between 100 m and 200 m. A slight decline leads to a broad trough between 200 m and 300 m before a rise to a second peak between 300 m and 400 m. There is then a sharp fall in abundance to a low at 500 m before a steady rise over the last 200 m of the beach.

The most significant departures from this trend occur in the 200381 transect. On that date the first peak is replaced by a slow, steady rise in abundance to a peak close to 250 m. The 100-200 m peak becomes more defined between 200381 and 290981 before decreasing slightly. The decrease is not sufficient to return the 310382 abundances to the 200381 level, however.

In some respects, these changes in the 100-200 m peak are mirrored in the 200-300 m trough. A high abundance on 200381 decreases over the subsequent seasons. In contrast to the peak, however, this trend continues right through to the next (310382) autumn.

Seasonal changes to the second peak are similar to those of the first. The changes are less extreme, however, and the principal seasonal difference is that the peak is narrower and occurs further down the beach in autumn (both 200381 and 310382).

The sharp decline in abundance from 400 m to 500 m is very similar in all seasons but the subsequent rise shows marked seasonal differences. There is a decrease from 200381 to 270681 followed by a sharp increase to 290981. That level is approximately retained in summer before a fall the following autumn when levels return close to those of the 200381 autumn.

Total species number (Fig. 4.16(b))

In contrast to the marked changes in overall abundance noted above, the number of species represented over the distribution transects remains relatively constant. There is a similar sharp rise in numbers over the first 50 m but over the rest of the beach the species number fluctuates only slightly about an average of 9 or 10.

Two small peaks in species number can be identified but these do not coincide with the peaks in overall community abundance. Instead, they are displaced slightly down the beach

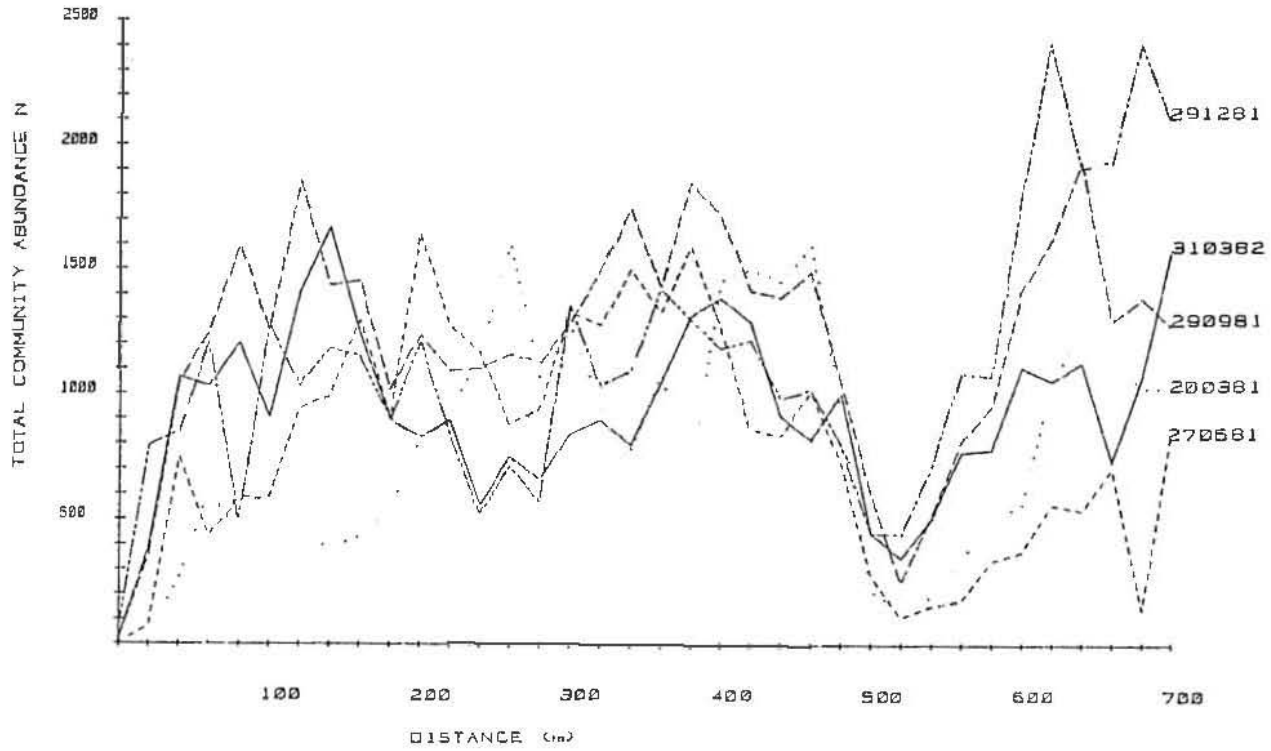


Fig. 4.16(a) Changes in the total community abundance along the distribution transects. Sampling dates are marked on the curves (as they are in the following figures).

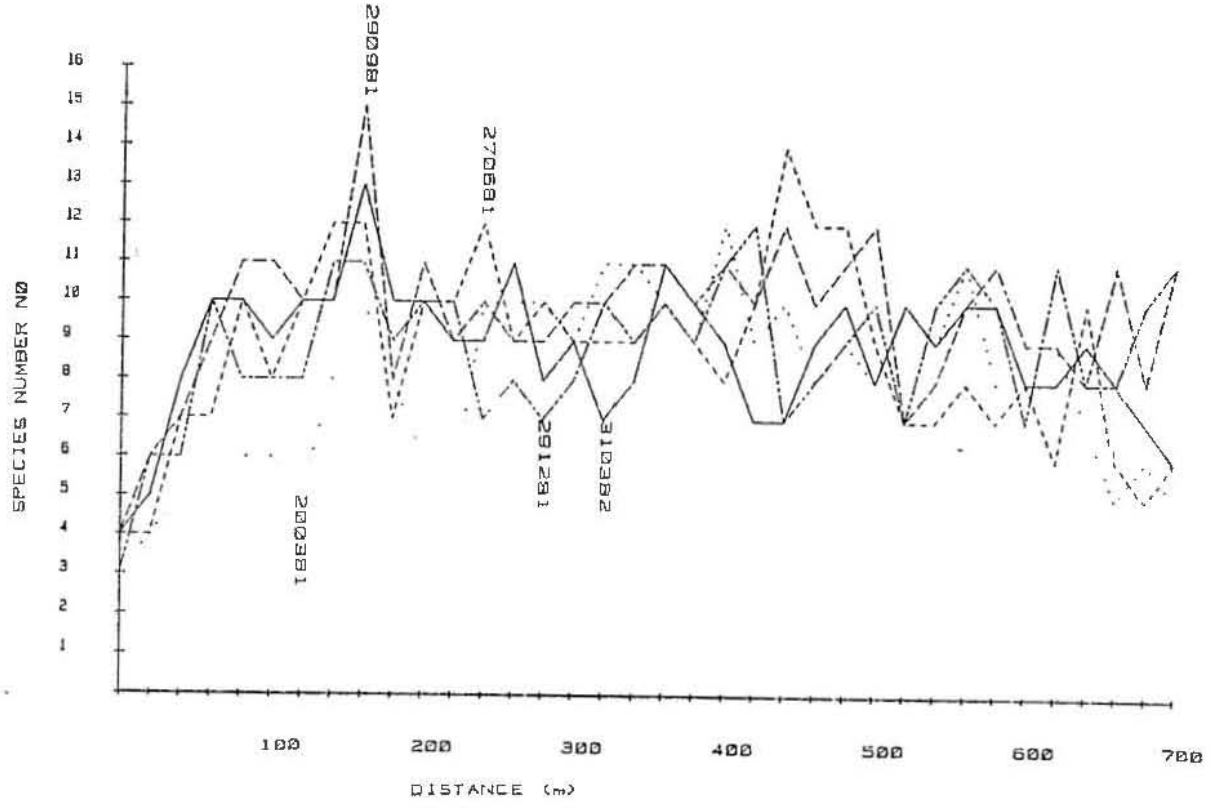


Fig. 4.16(b) Changes in the number of species represented along the distribution transects.

from those peaks. There are minimal troughs associated with the abundance troughs and the rapid increases in abundance below 500 m are not paralleled by increases in the number of species represented.

Again, the pattern on 200381 shows the major deviations from the general trend, particularly high on the beach where species number remains comparatively low until about 200 m. Minor deviations occur between 200 m and 300 m and between 400 m and 500 m where summer and autumn species numbers are low and between 600 m and 700 m where autumn and winter species numbers are low.

Species diversity coefficients (Figs. 4.16(c-e))

Except at the extreme top of the beach (0 m to 50 m), the changes in species diversity, heterogeneity and evenness approximately parallel the trends in the beach profile (Fig.2.1) and approximately mirror the changes in overall abundance (Fig. 4.16(a)). Thus, there is a decline in the coefficients between 50 m and 200 m prior to an increase leading to a peak slightly up-beach of the zone 3 beach ridge. This peak, in fact, appears to be a double peak with the secondary part occurring slightly down-beach from the zone 3 ridge.

There is a sharp peak in the coefficients centered around 500 m, with the upper beach side of the peak being more defined than the lower beach side. The latter area exhibits the greatest seasonal variation of coefficients and the 200381 and 270681 values are considerably higher than those of the other dates. Although the abundance and species number curves for 200381 are markedly different to those in other seasons, the difference is only slight for the diversity coefficients; the 200381 (and, below 500 m, the 270681) coefficients tend to be slightly greater than those of other seasons.

4.3.2.2 Species less 0 mm animals diversity (Fig. 4.17)

Overall community less 0 mm animals abundance (Fig. 4.17(a))

The effect of removing juvenile (0 mm) animals from the preceding analysis is considerable. The most obvious effect is the dissappearance of the 500 m trough, indicating a relative intolerance of juveniles to exposure. Also, the second peak (between 300 m and 400 m) is greatly reduced. These changes reflect the increased proportion of juveniles in the lower beach areas. The general result is for the flucuations, both within and between seasons, to be damped. The relative seasonal differences are approximately retained.

Total species less 0 mm animals number (Fig. 4.17(b))

There is little difference between Figs. 4.16(b) and 4.17(b), indicating that the 0 mm animals are not predominantly responsible for species representation. There is a

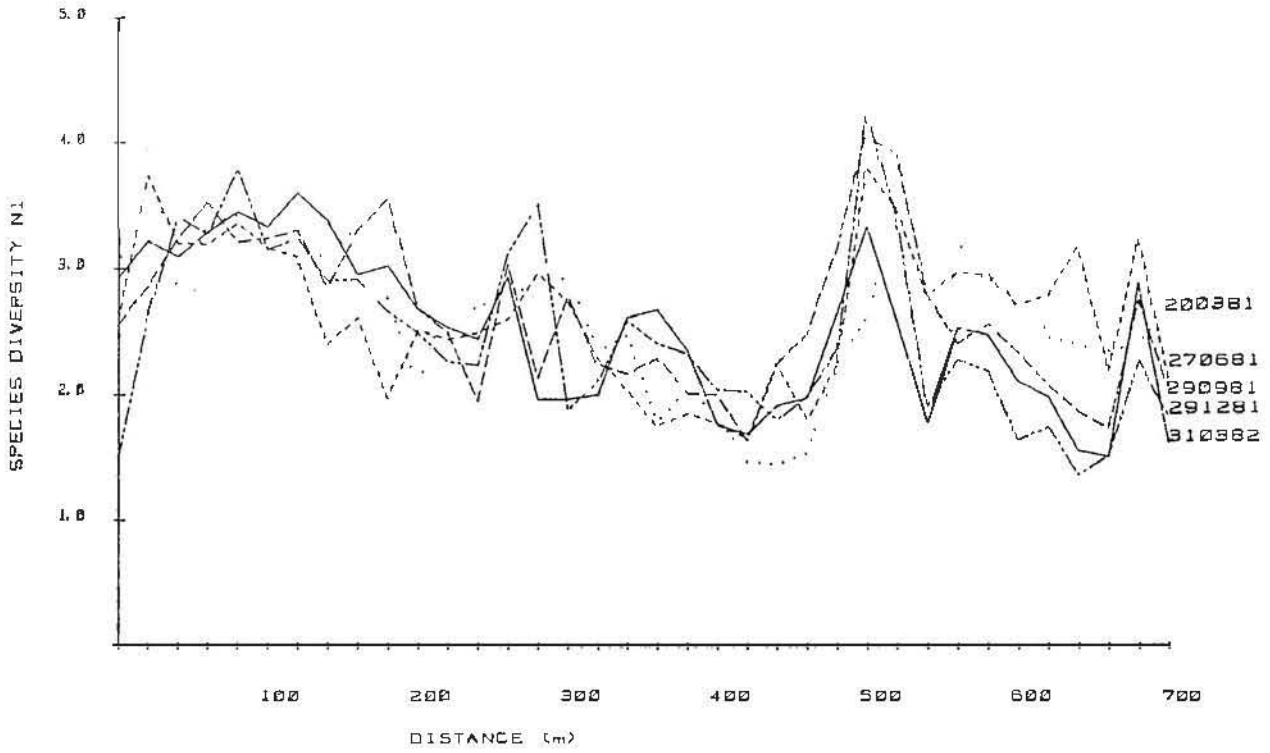


Fig. 4.16(c) Changes in the species diversity along the distribution transects.

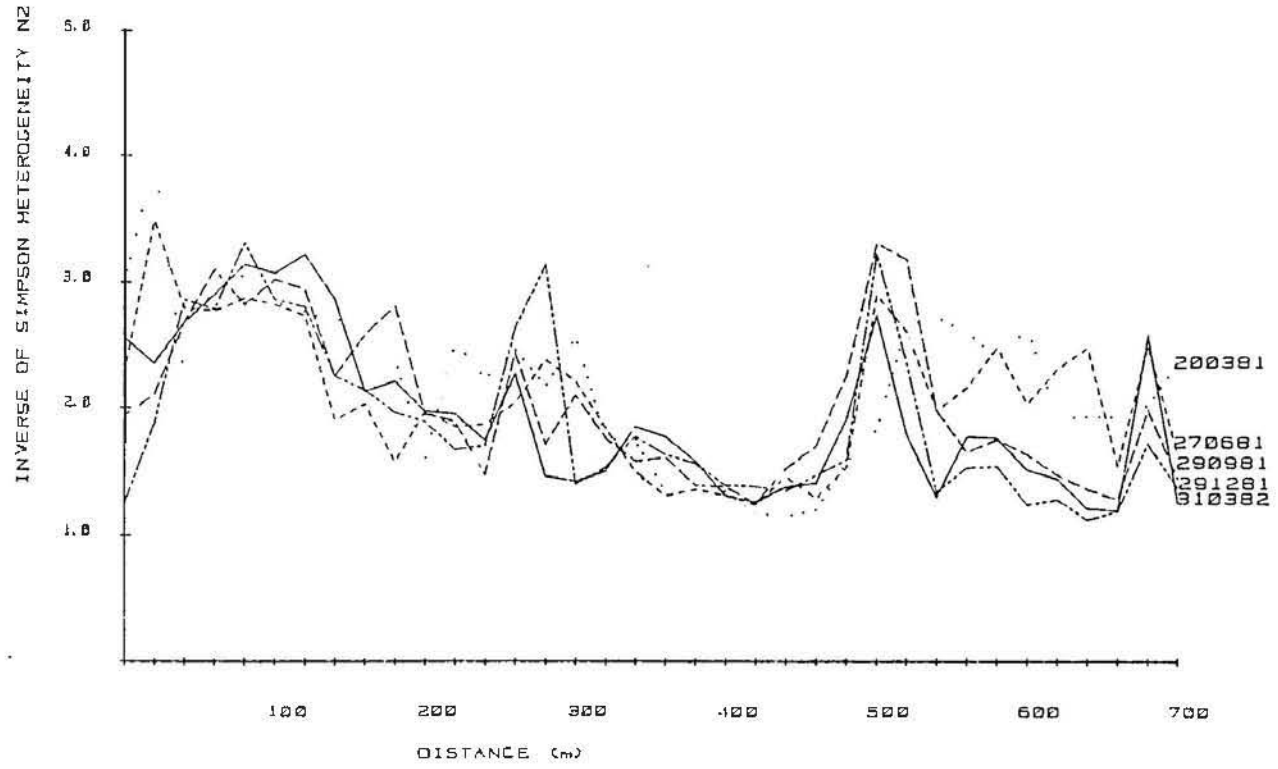


Fig. 4.16(d) Changes in the inverse of species heterogeneity along the distribution transects.

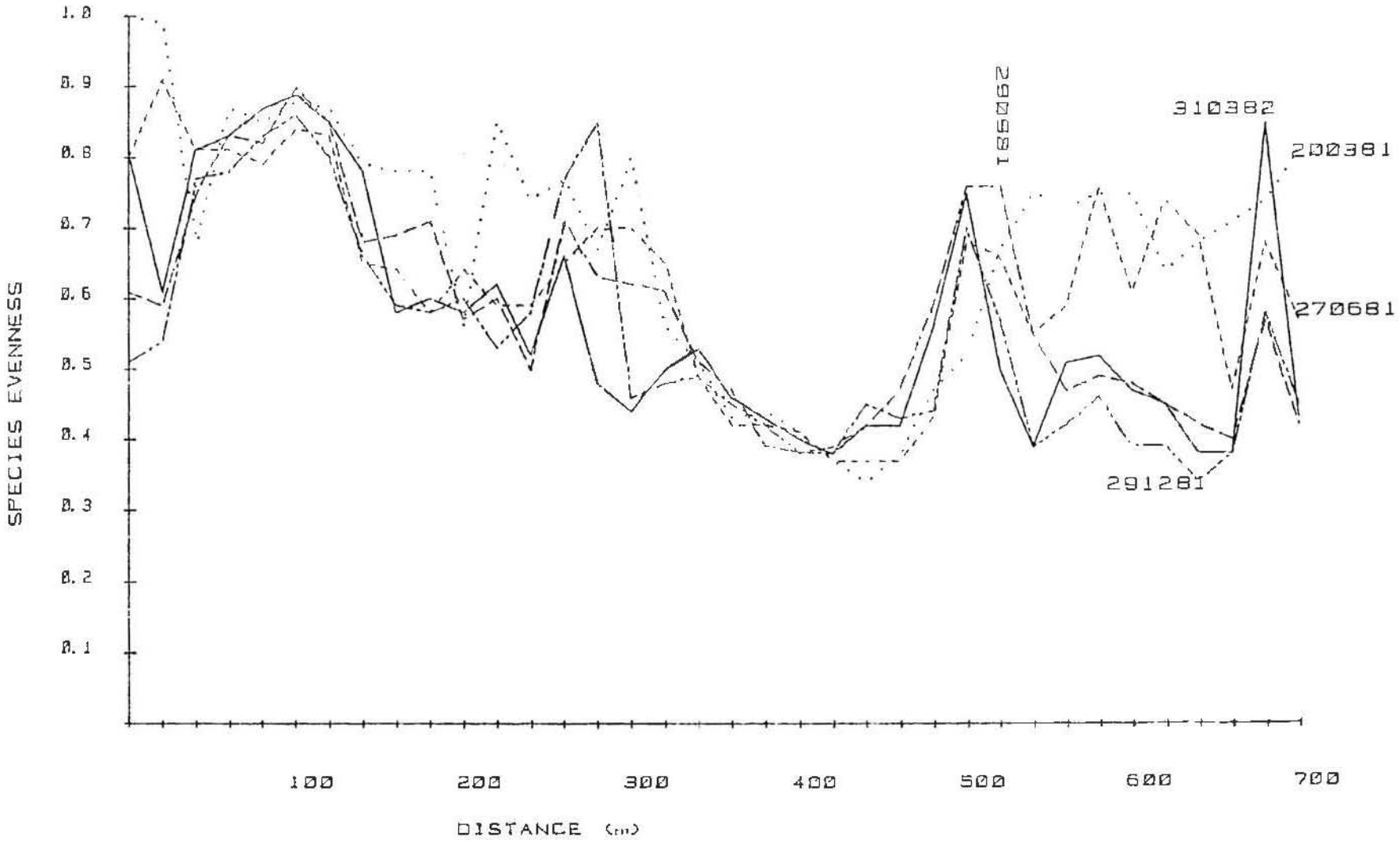


Fig. 4.16(e) Changes in the species evenness along the distribution transects.

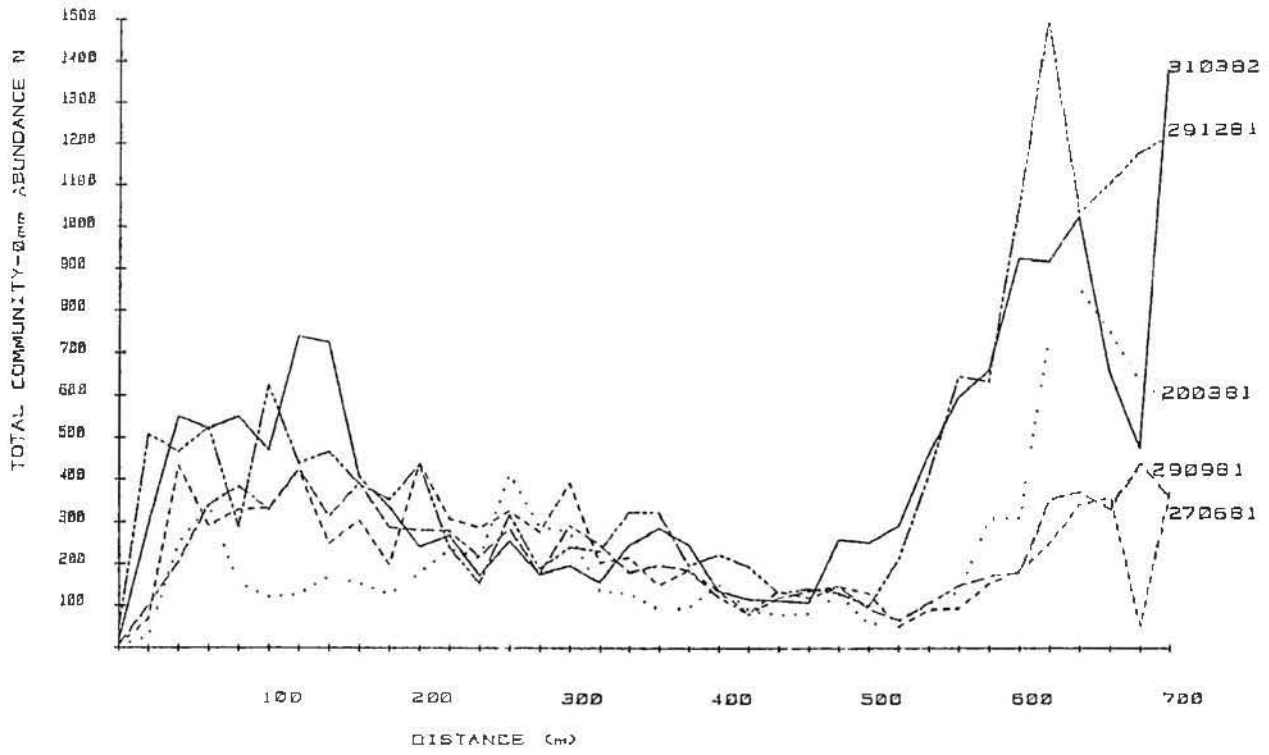


Fig. 4.17(a) Changes in the total community abundance, excluding 0 mm animals, along the distribution transects.

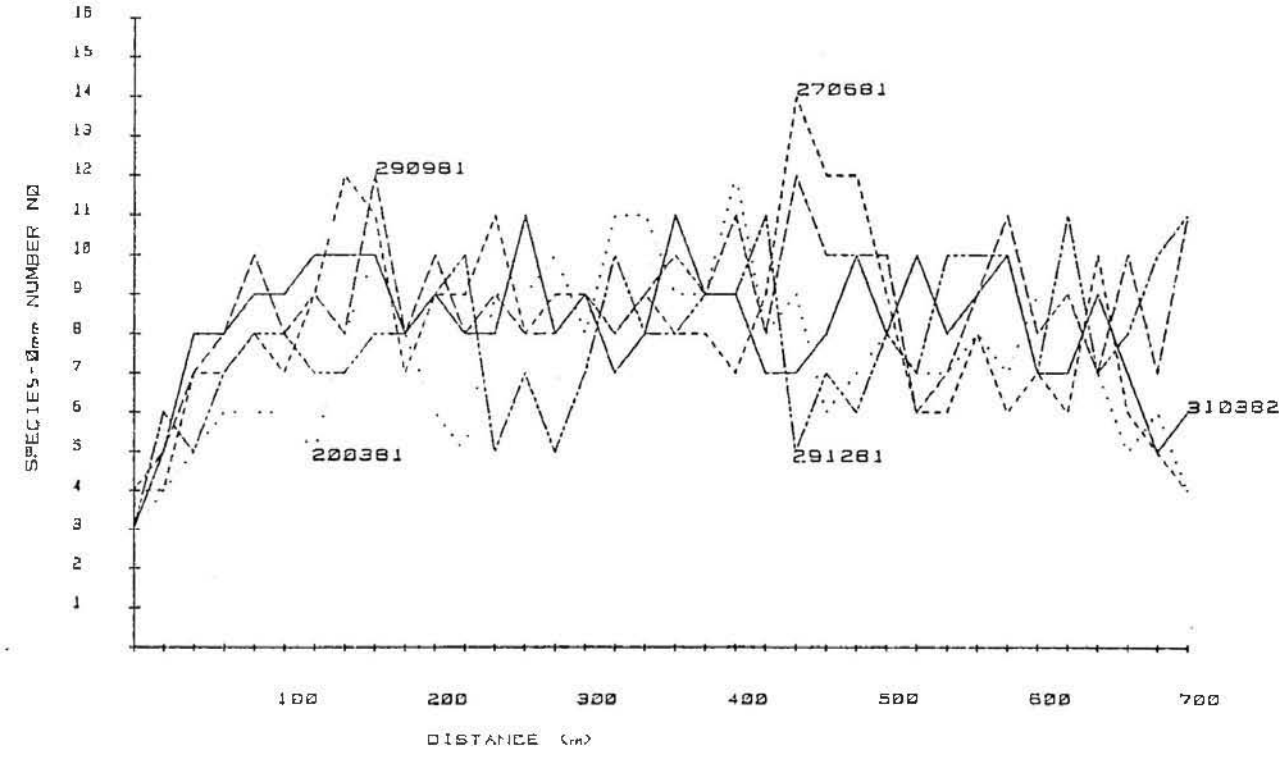


Fig. 4.17(b) Changes in the number of species, excluding 0 mm animals, represented along the distribution transects.

slight decrease (from 9-10 to 8-9) in the average level about which the species numbers fluctuate but the general patterns remain very similar.

Species less 0 mm animals diversity coefficients (Figs. 4.17(c-e))

As with the overall abundance patterns, the effect of neglecting the juvenile animals when calculating the apparent species diversity coefficients is considerable. The multiple peaks are replaced by a large single peak, centred close to 400 m where previously there had been a major trough. The other peaks and troughs have been replaced also, by slight troughs and peaks. The result is an area of very gradual increase in the coefficients between 20 m and 300 m, followed by a more rapid increase in most seasons to a peak between 400 m and 500 m. There is a subsequent steep decline to 700 m.

The relative differences between seasons are not strictly retained. The 200381 curves, in particular, have come to lie below those of the other seasons in areas where they previously lay above. Also, the 290981 curves have increased their position, particularly below 450 m. Previously, the large variation among the seasonal curves was restricted to between 500 m and 700 m but, with the removal of the 0 mm animals, the variability is high between 300 m and 700 m.

While Figs. 4.16 (a), (b) and (c) are fundamentally similar, the combination of Figs. 4.17(c) and (d) produce a dissimilar Fig. 4.17(e). The evenness coefficients of the assemblage without the 0 mm animals shows only a gradual decline over most of the beach, without the mid-beach peak apparent in the diversity and heterogeneity coefficients. The relative positions of the seasonal curves are retained from Figs. 4.17(c) and (d) to (e), however

4.3.2.3 Hierarchical diversity (Fig. 4.18)

Total community class number (Fig. 4.18(a))

In contrast to the relatively constant number of species represented along the distribution transects (Fig. 4.16(b)), the class representation (pooled for all species) shows a trend from a minimum close to 0 m through broad peak (of about 45 classes) between 100 m and 400 m followed by a steady decline from 400 m to 700 m. Like the species number, however, the class number appears little affected by the major topographical features of the beach, there being only a minor trough associated with the ridge at 500 m, for example.

The seasonal variability is greatest below 400 m and, as with the species number, the 200381 transect shows the largest deviations from the main trend. This is most noticable between 100 m and 250 m when the 200381 values are considerable less than those of the other seasons.

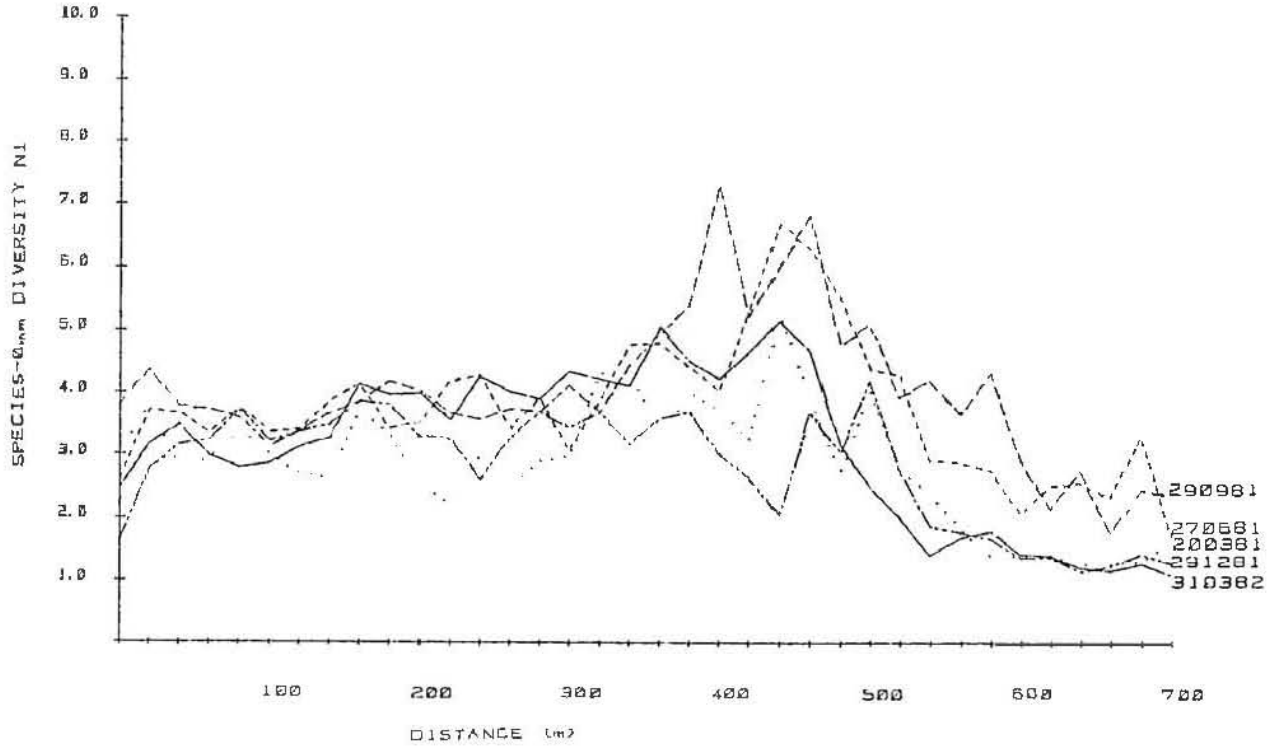


Fig. 4.17(c) Changes in the species diversity, excluding 0 mm animals, along the distribution transects.

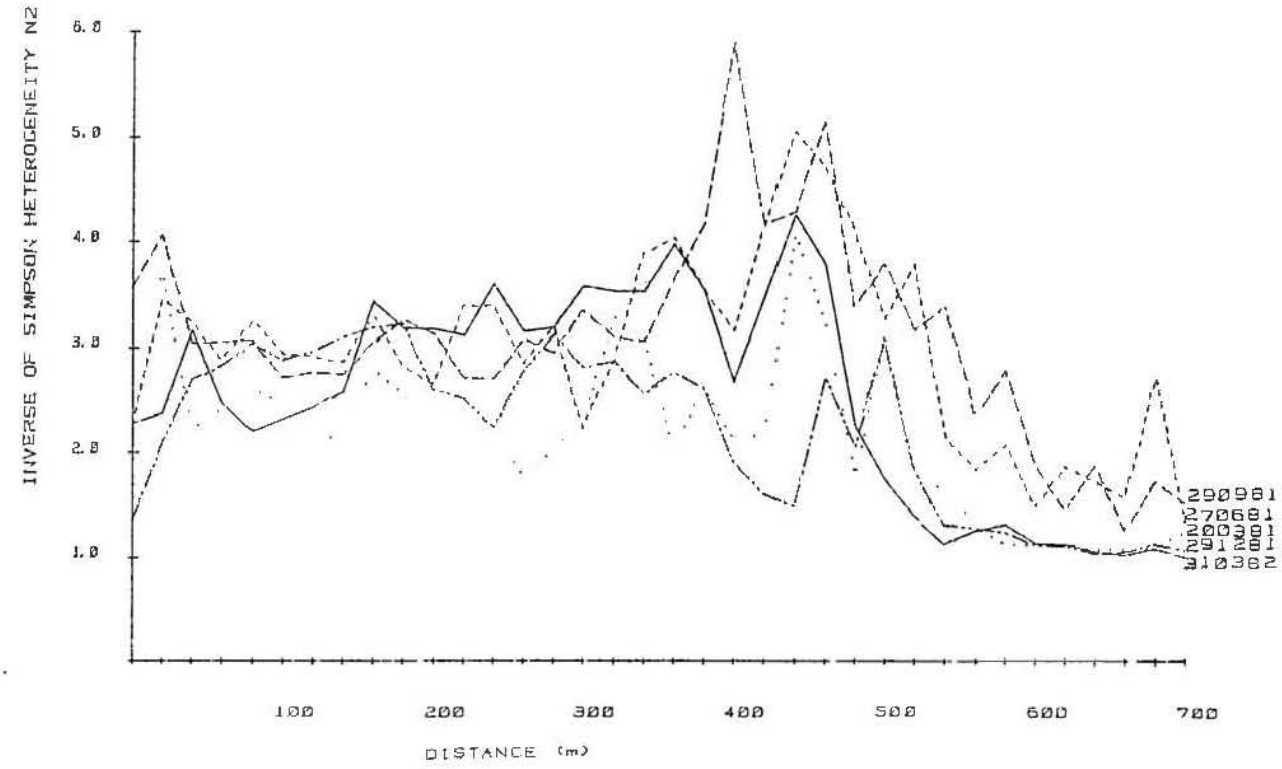


Fig. 4.17(d) Changes in the inverse of species heterogeneity, excluding 0 mm animals, along the distribution transects.

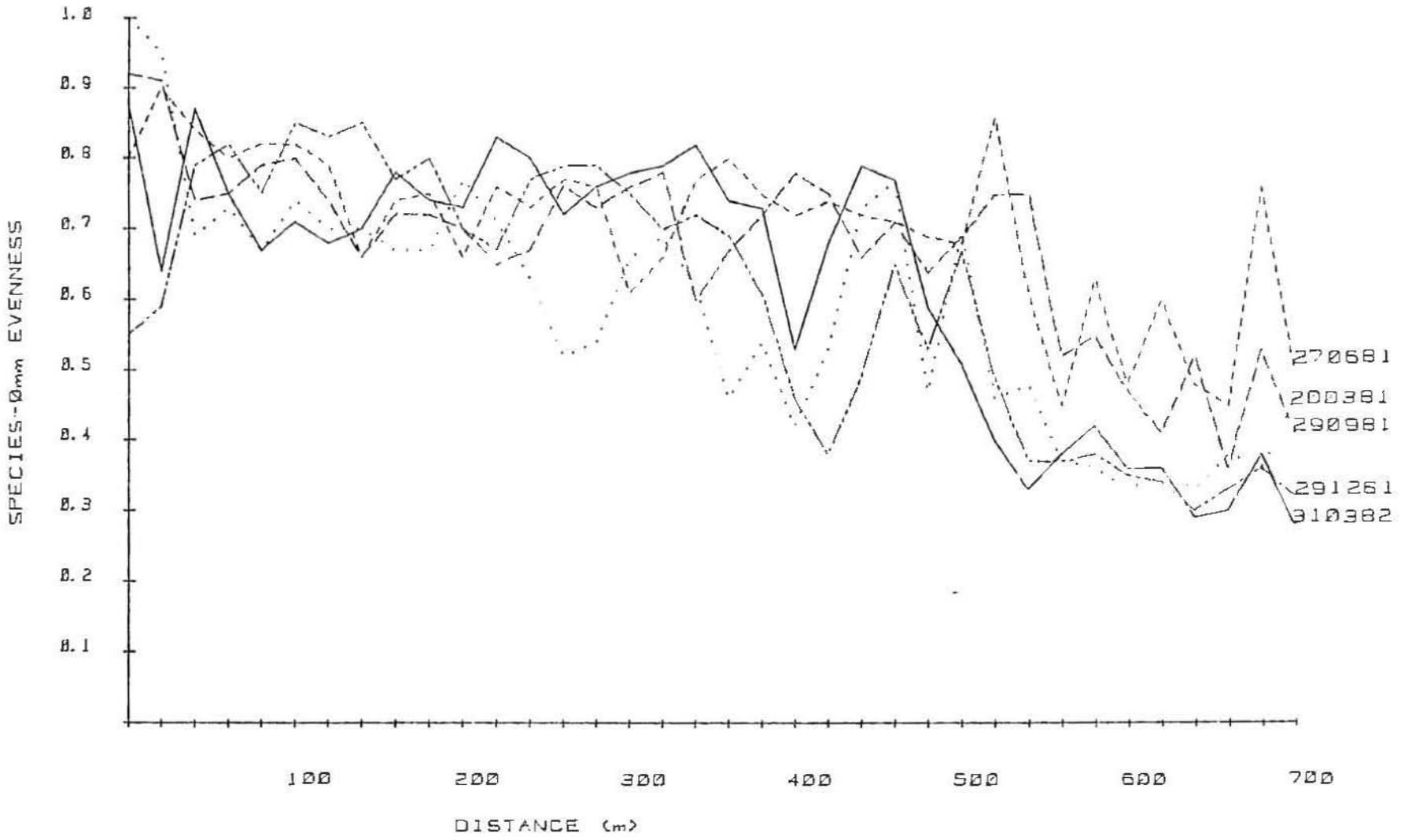


Fig. 4.17(e) Changes in the species evenness, excluding 0 mm animals, along the distribution transects.

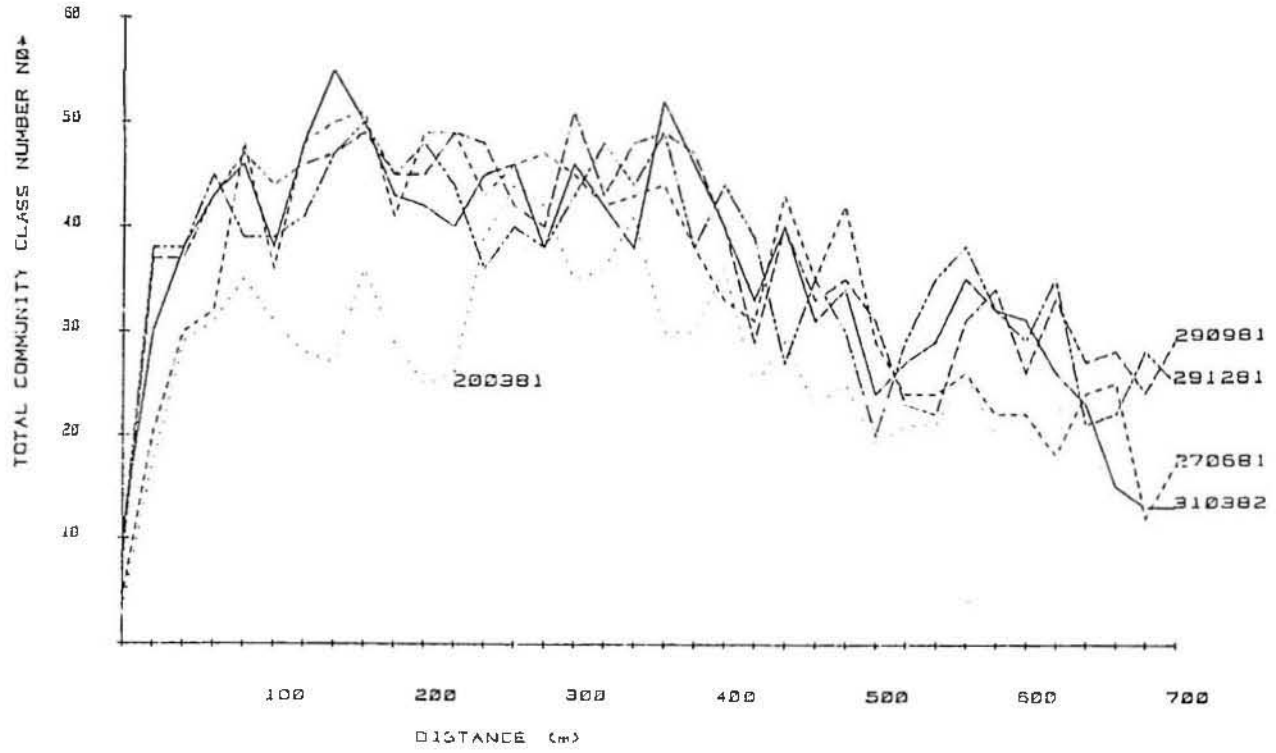


Fig. 4.18(a) Changes in the total number of size classes (all species pooled) represented along the distribution transects.

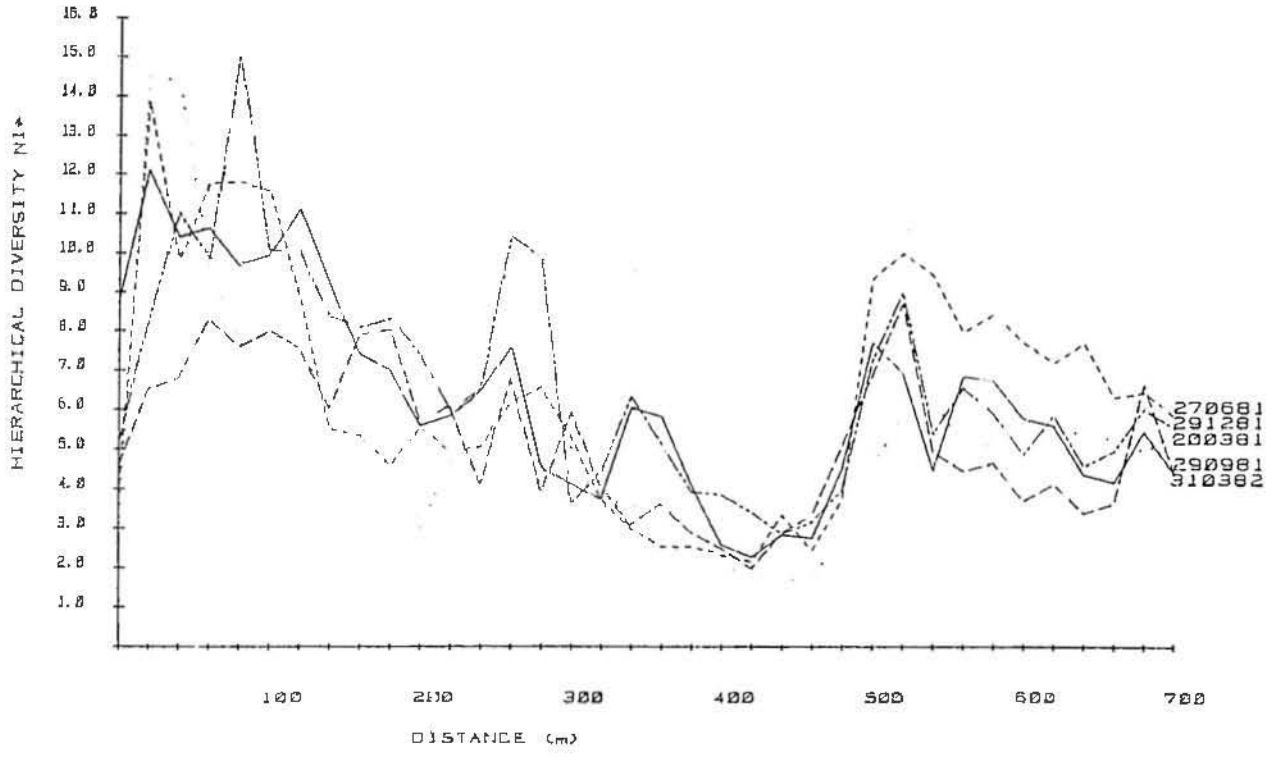


Fig. 4.18(b) Changes in the size class diversity (all species pooled) along the distribution transects.

Hierarchical diversity coefficients (Fig. 4.18(b-d))

The trends of the hierarchical diversity coefficients are basically similar to those of the species coefficients (Figs. 4.16(c-e)). The major difference is the greater seasonal variability shown by the hierarchical coefficients in the upper regions of the beach, above 200 m. Also of note are the comparatively low values of the hierarchical coefficients in the upper and lower 200 m of the beach during spring.

4.3.2.4 *Anapella* **Hill series** (Fig. 4.19)

For convenience, total *Anapella* abundances are shown in Fig. 4.19(a).

Anapella class representation (Fig. 4.19(b))

The number of *Anapella* size classes represented in the distribution transects generally shows a rapid increase between 0 m and 50 m to reach a plateau maximum (of 12-13) that is approximately maintained between 50 m and 400 m. Following 400 m the number declines rapidly before the rate of decrease levels out betwen 400 m and 700 m. The upper beach slope and the beach ridge at 500 m are effectively upper and lower bounds to the plateau. The lack of recovery of the class numbers below the beach ridge are concomitant with the failure to recover shown by the overall *Anapella* abundance.

There are no consistent seasonal trends other than the obvious departures shown during the 200381 autumn when there is a marked trough in class number between 50 m and 250 m; class numbers are lower overall in that season.

Anapella diversity coefficients (Figs. 4.19(c-e))

The plateau in class numbers noted above are associated with a flat trough in the diversity coefficients, although the latter extends almost 100 m (from 400 m to 500 m) further down the beach.

Two peaks in the within-species diversity and heterogeneity coefficients exist, the first between 50 m and 150 m and the second between 500 m and 700 m. The second lies in the area of very low abundance and low class numbers and the first also appears to be associated with decreases in those two parameters. The combination of diversity and heterogeneity leads to a reversal of the 0-50 m ascent in the evenness term, producing a sharp decline in that region and a consequent removal of the first peak. The second peak of the evenness coefficient is also less distinct, being replaced by an area of widely fluctuating values that show a general upward trend.

The above pattern remains basically the same over all seasons, with the major departures again occurring during the 200381 autumn when the coefficients are

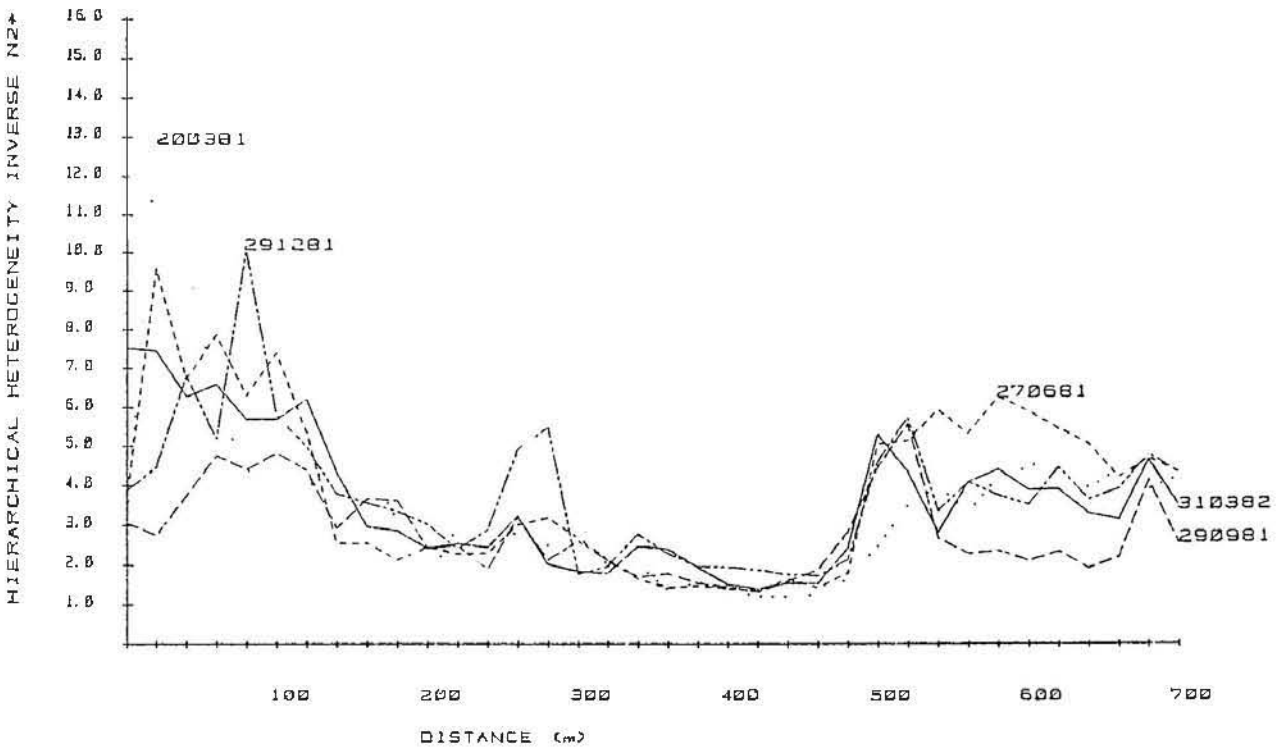


Fig. 4.18(c) Changes in the inverse of size class heterogeneity (all species pooled) along the distribution transects.

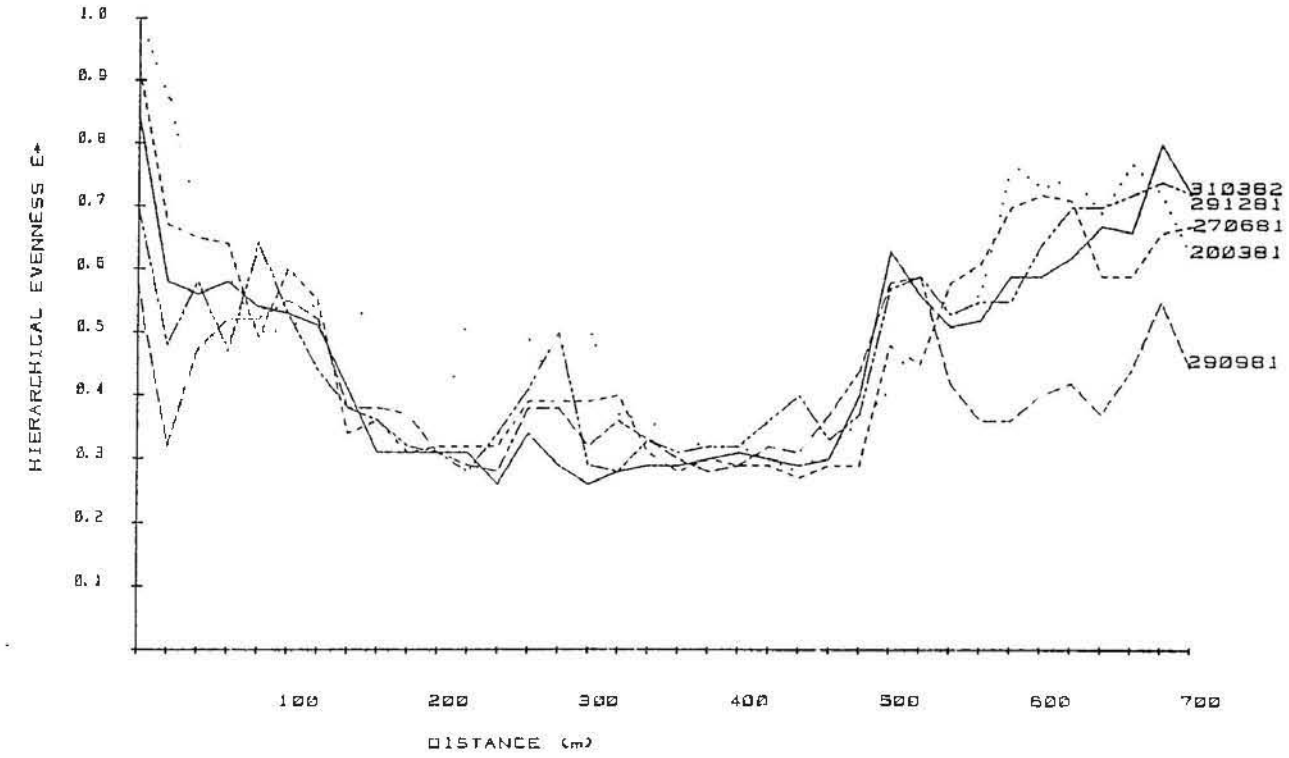


Fig. 4.18(d) Changes in the size class (hierarchical) evenness (all species pooled) along the distribution transects.

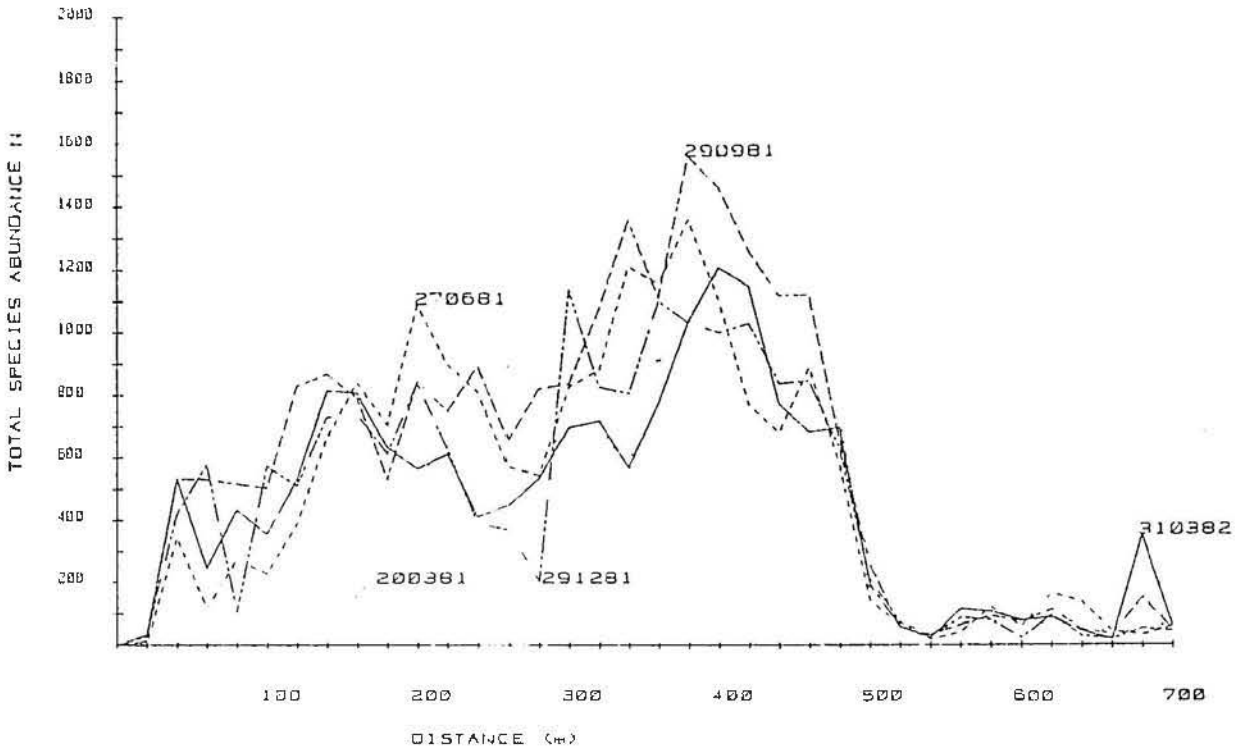


Fig. 4.19(a) Changes in the total *Anapella* abundance along the distribution transects.

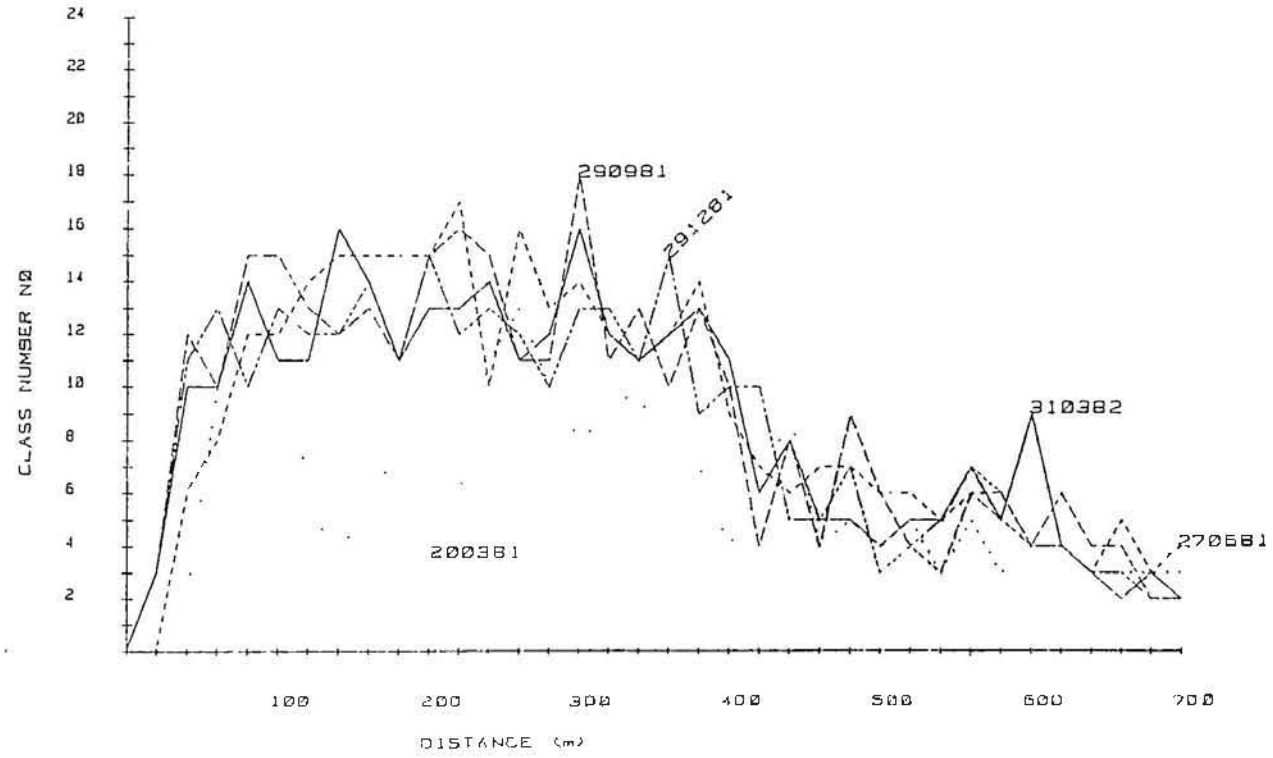


Fig. 4.19(b) Changes in the number of *Anapella* size classes represented along the distribution transects.

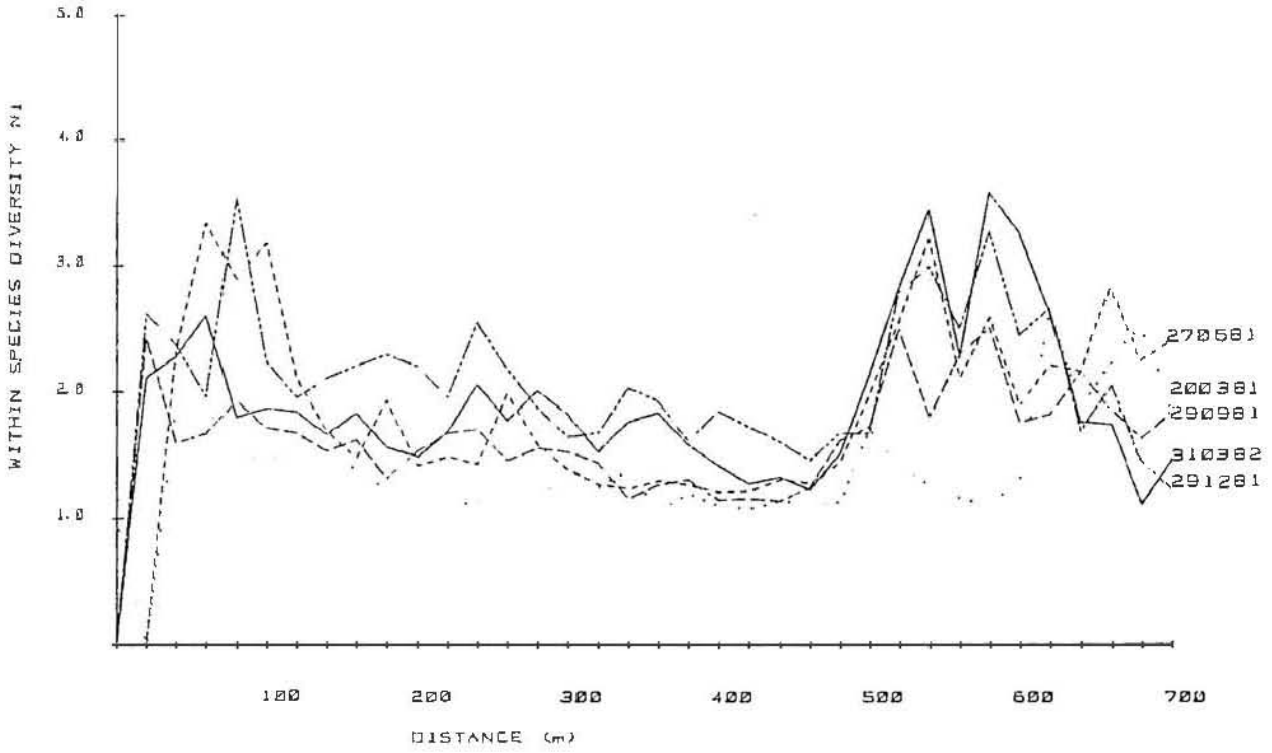


Fig. 4.19(c) Changes in the size class diversity of *Anapella* along the distribution transects.

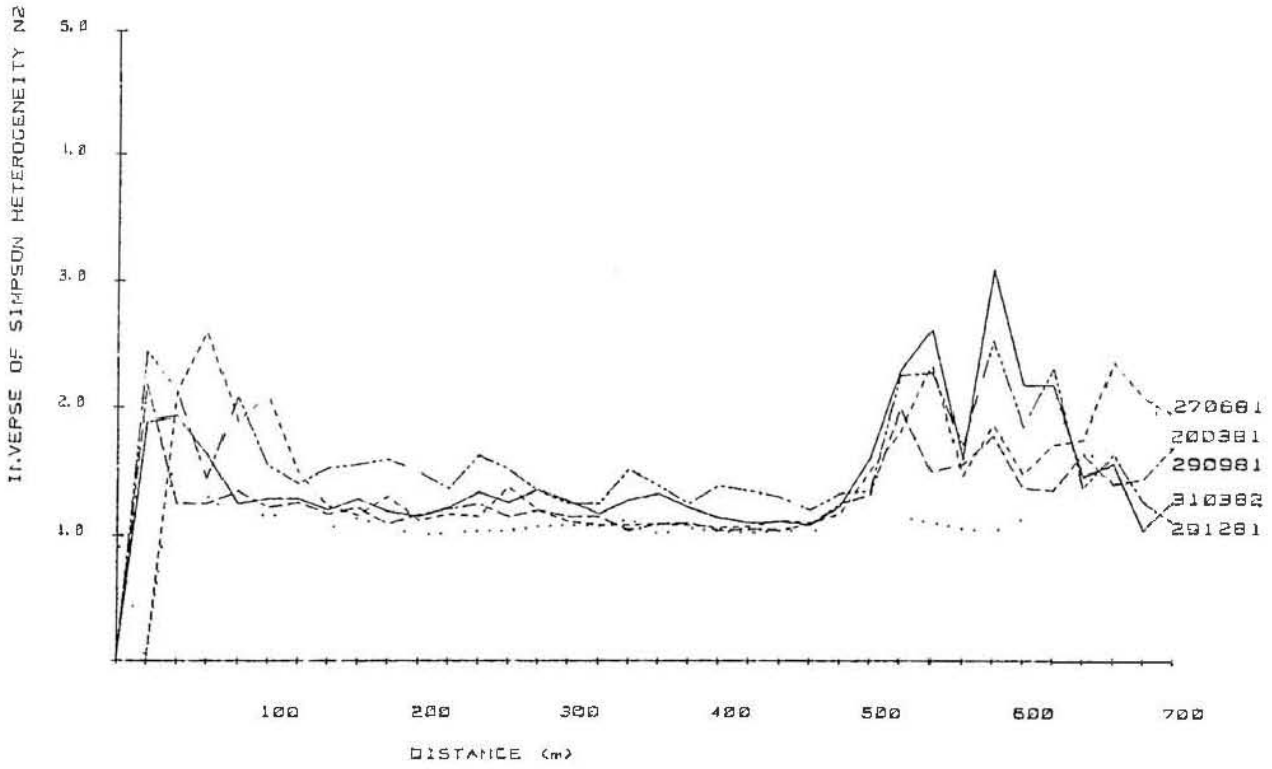


Fig. 4.19(d) Changes in the inverse of *Anapella* size class heterogeneity along the distribution transects.

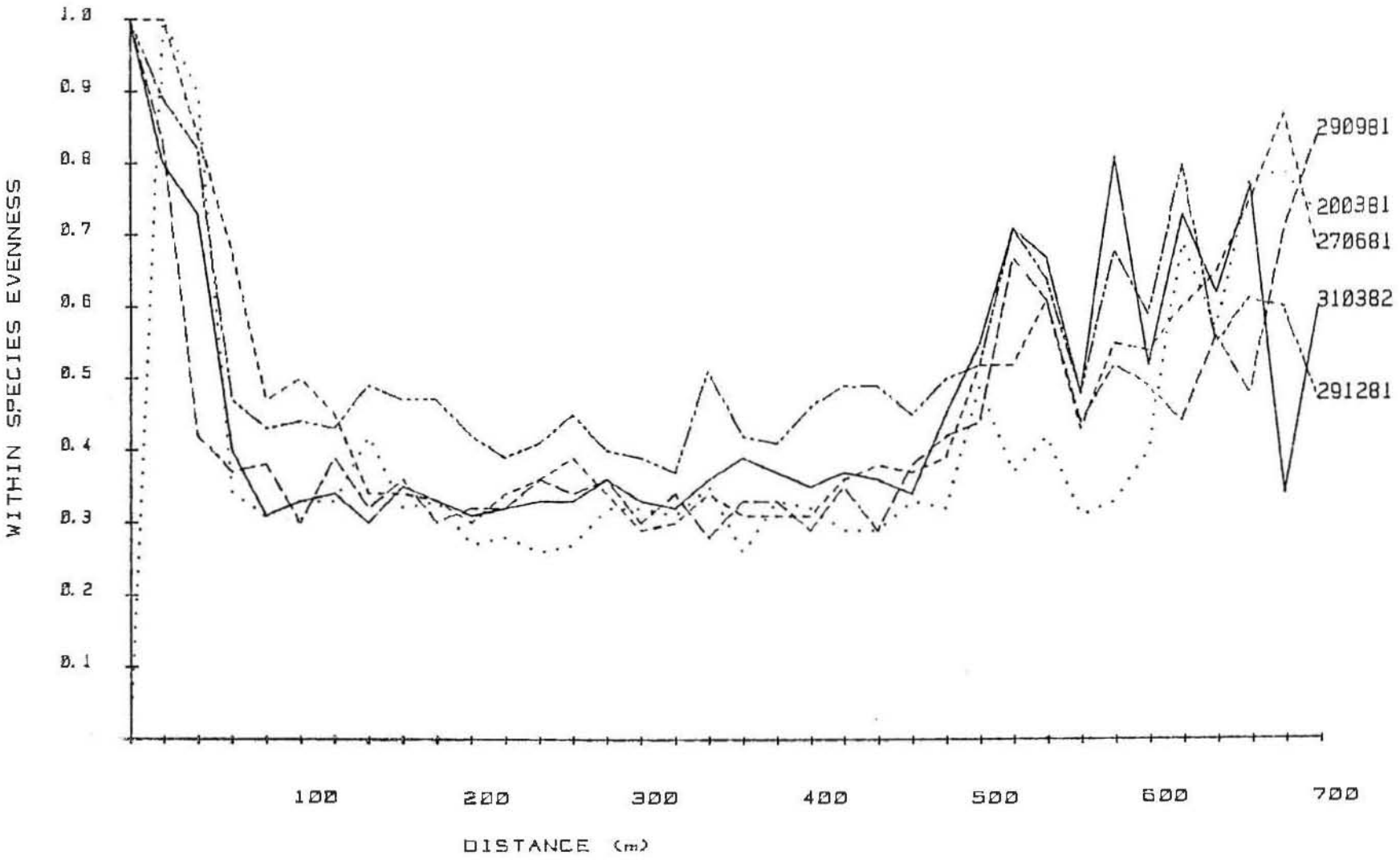


Fig. 4.19(e) Changes in the size class evenness of *Anapella* along the distribution transects.

consistently lower than during other seasons.

4.3.2.5 *Katelysia* Hill series (Fig. 4.20)

Total *Katelysia* abundances are shown in Fig. 4.20(a).

Katelysia class representation (Fig. 4.20(b))

The number of *Katelysia* size classes represented increases below 300 m to a peak slightly below the 500 m mark before declining again towards 700 m. The maximum class number is approximately 10 but the average is close to 5 (out of a possible 30). This contrasts with *Anapella*, which averages about 10 out of a possible 24 over much of the beach.

There are no consistent seasonal patterns in the class representation although the 200381 autumn values are generally the lowest.

Katelysia diversity coefficients (Figs. 4.20(c-e))

The within-species diversity and heterogeneity coefficients exhibit 2 peaks. The first peak is poorly defined but lies between 250 m and 350 m, the area of initial increase from the very low upper beach abundances. The combination of these coefficients removes the first peak in the evenness coefficient. The evenness terms are non-trivial only below 300 m where they stabilise following wide, irregular fluctuations.

The coefficients remain relatively constant between 350 m and 450 m but then increase sharply to the second peak centred close to 540 m. The within-species diversity and heterogeneity coefficient second peaks are highest in the 200381 autumn, the winter and the summer. The high summer peak is lost in the evenness term, however.

4.3.2.6 *Hydrococcus* Hill series (Fig. 4.21)

Total *Hydrococcus* abundances are shown in Fig. 4.21(a).

Hydrococcus class representation (Fig. 4.21(b))

Hydrococcus class representation is consistently high over most of the beach with 4 being a pivotal number. Above 200 m all classes are frequently present except for the uppermost 20 m. Between 200 m and 500 m all seasons show fluctuations between 3 and 4 classes but below 500 m there is little deviation from 4.

The above three regions (20-200, 200-500, 500-700 m) are associated with the principal abundance features. The upper beach abundance peak is the area where all classes are present, the broad area of low abundance has class representation fluctuating between 3 and 4 and the high abundances low on the beach are consistently associated with 4 classes.

Hydrococcus diversity coefficients (Fig. 4.21(c-e))

The diversity coefficients of *Hydrococcus* do not exhibit the well defined trends

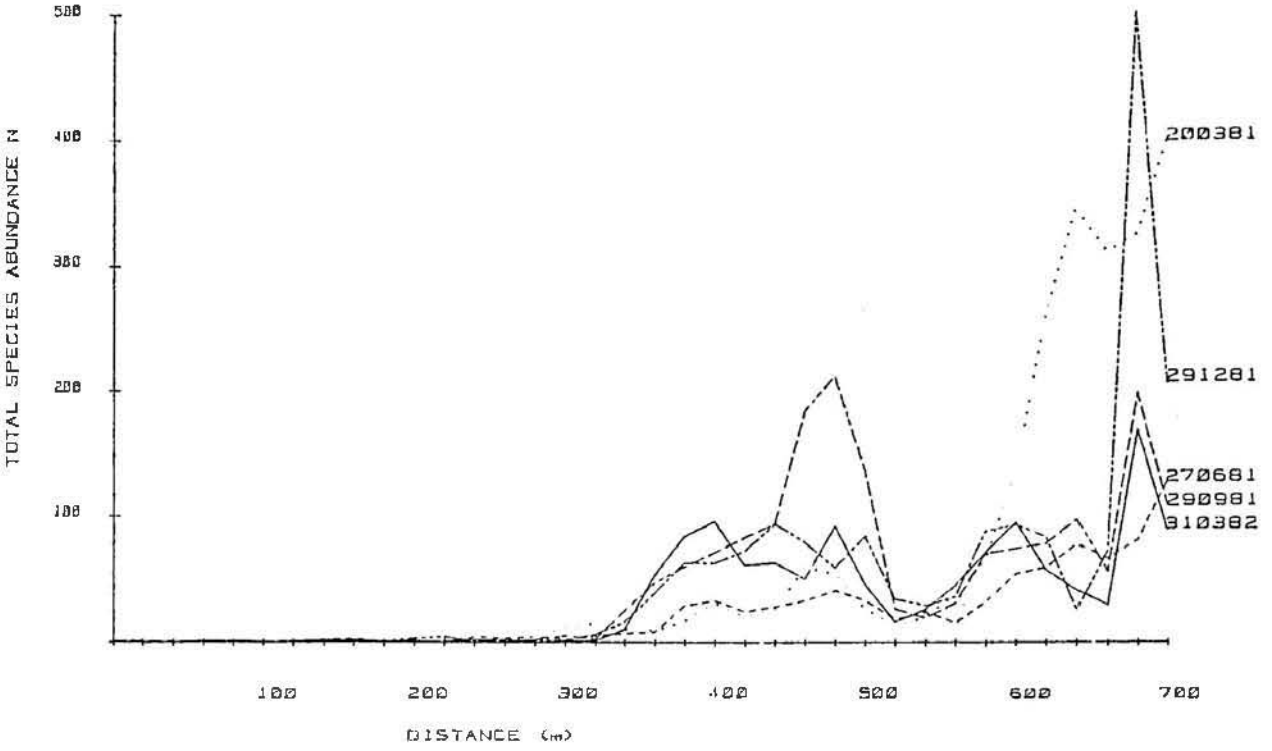


Fig. 4.20(a) Changes in the total *Katelysia* abundance along the distribution transects.

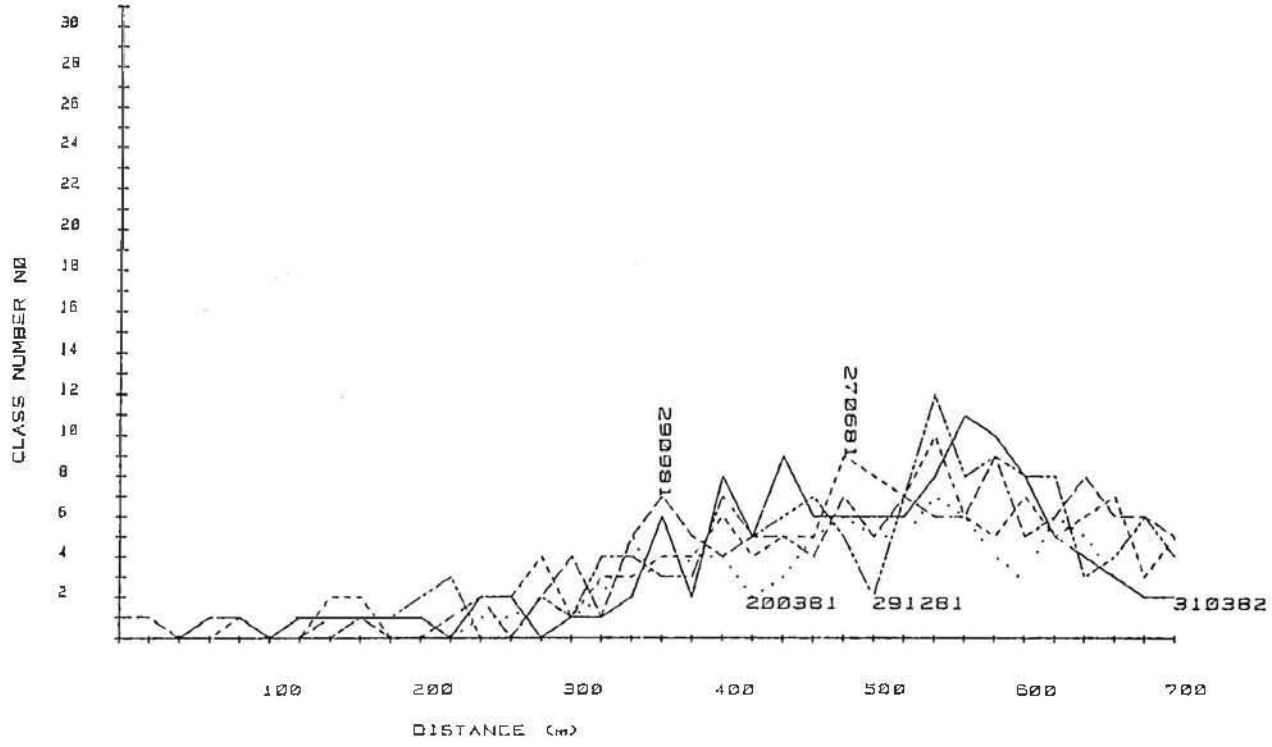


Fig. 4.20(b) Changes in the number of *Katelysia* size classes represented along the distribution transects.

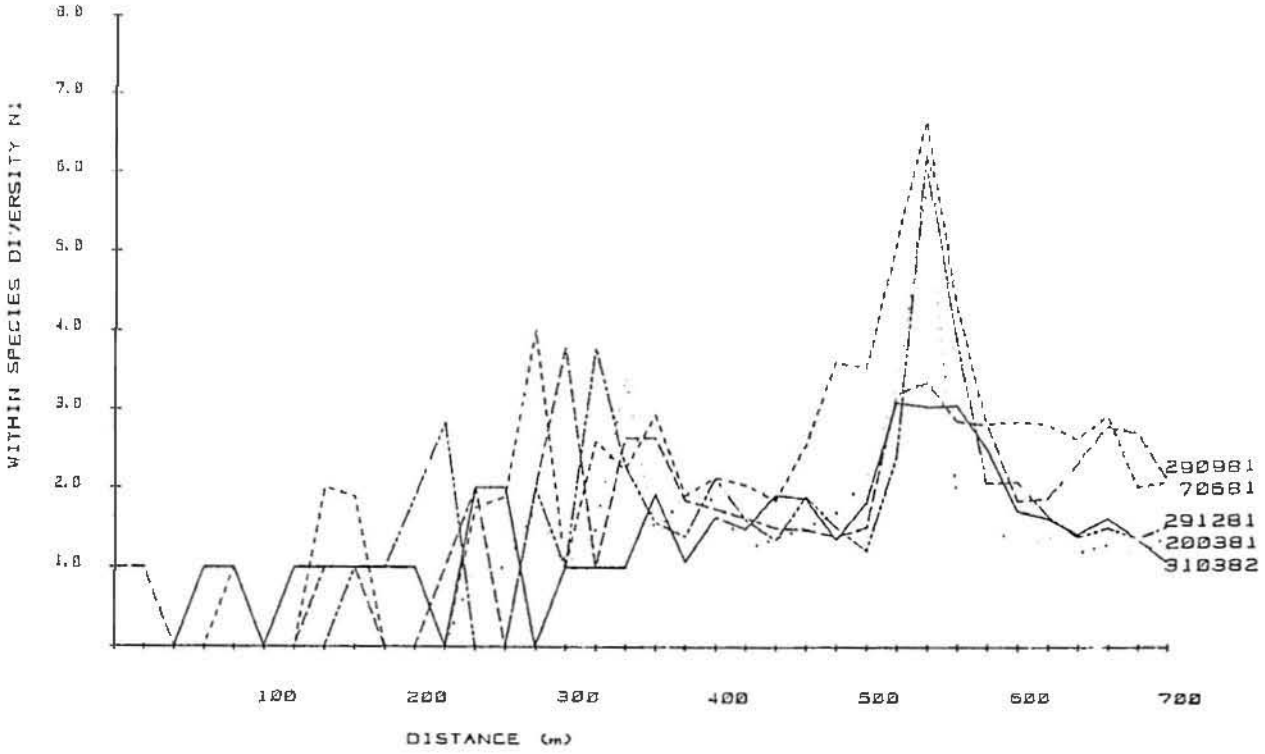


Fig. 4.20(c) Changes in the size class diversity of *Katelysia* along the distribution transects.

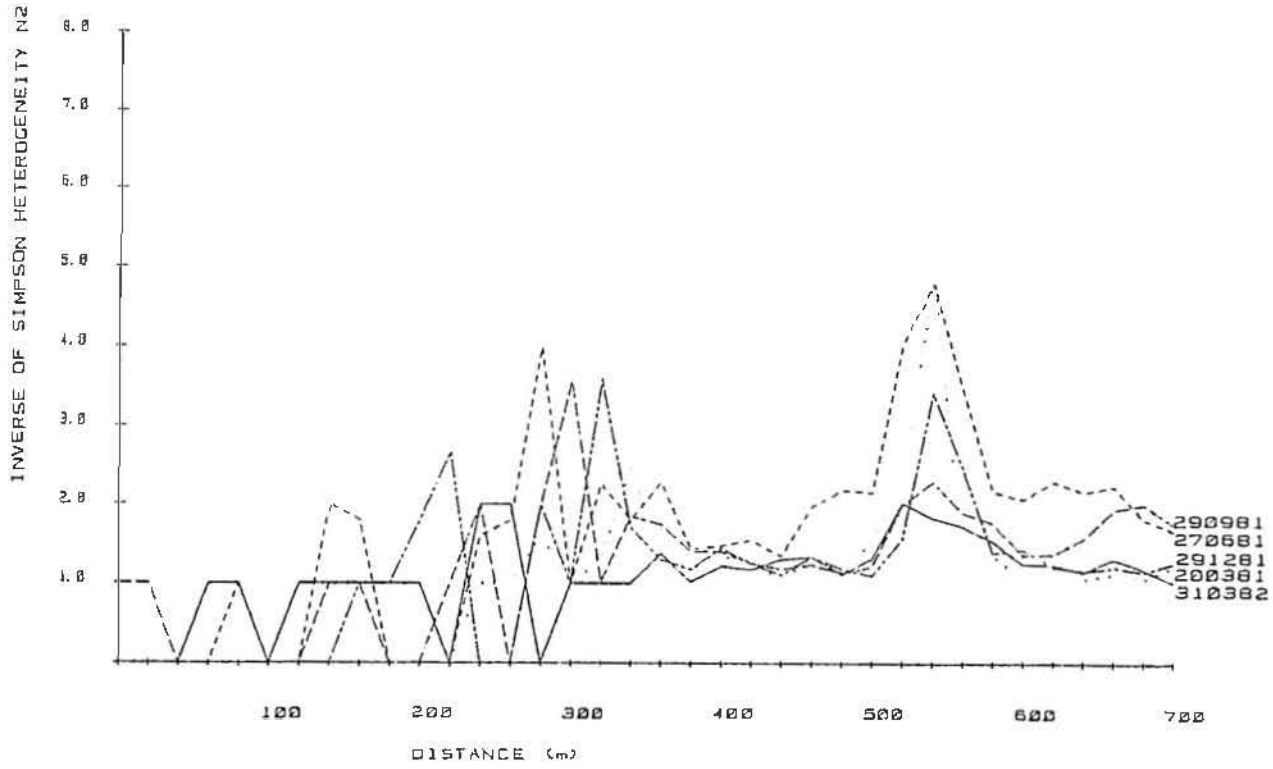


Fig. 4.20(d) Changes in the inverse of *Katelysia* size class heterogeneity along the distribution transects.

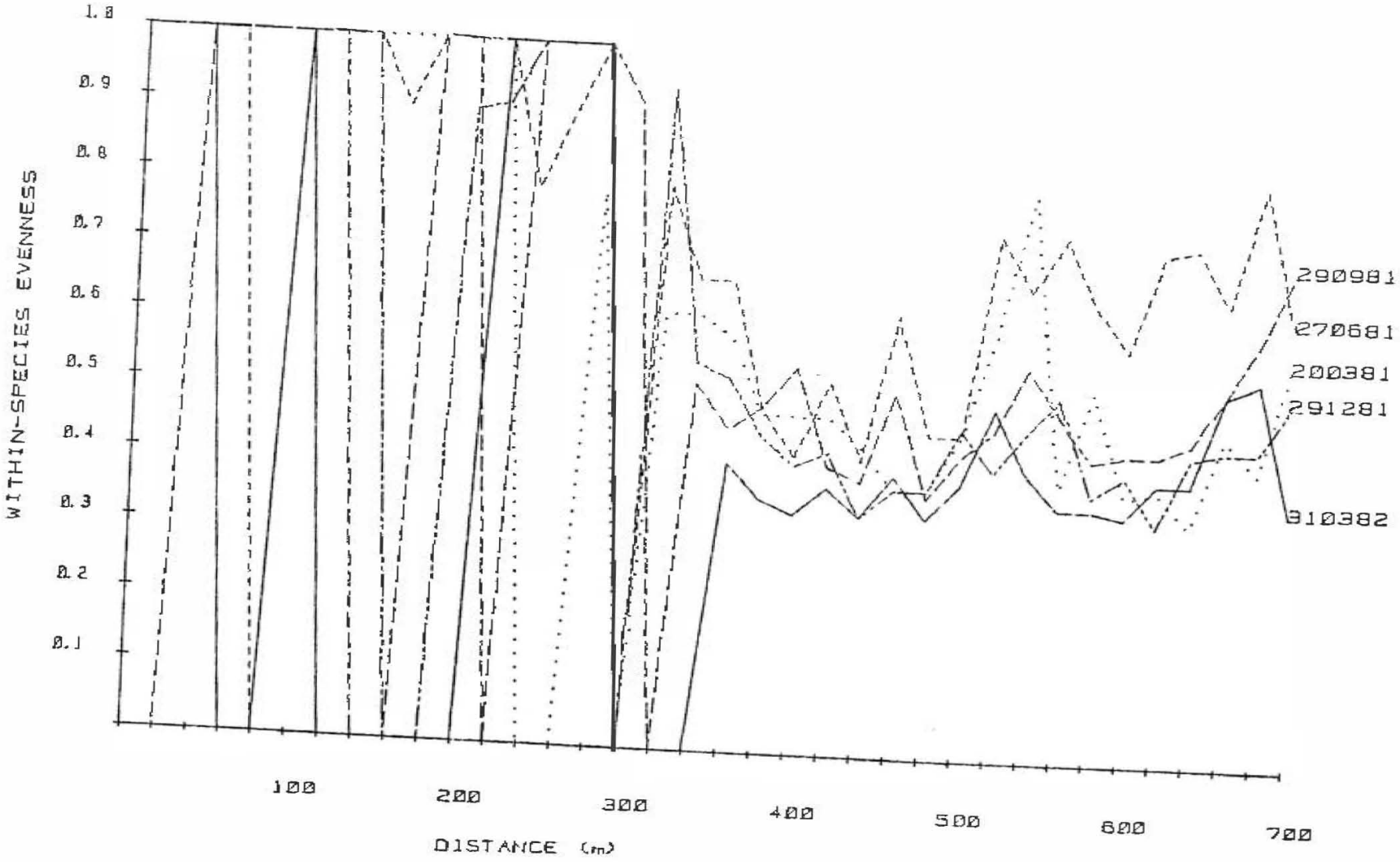


Fig. 4.20(e) Changes in the size class evenness of *Kalelysia* along the distribution transects.

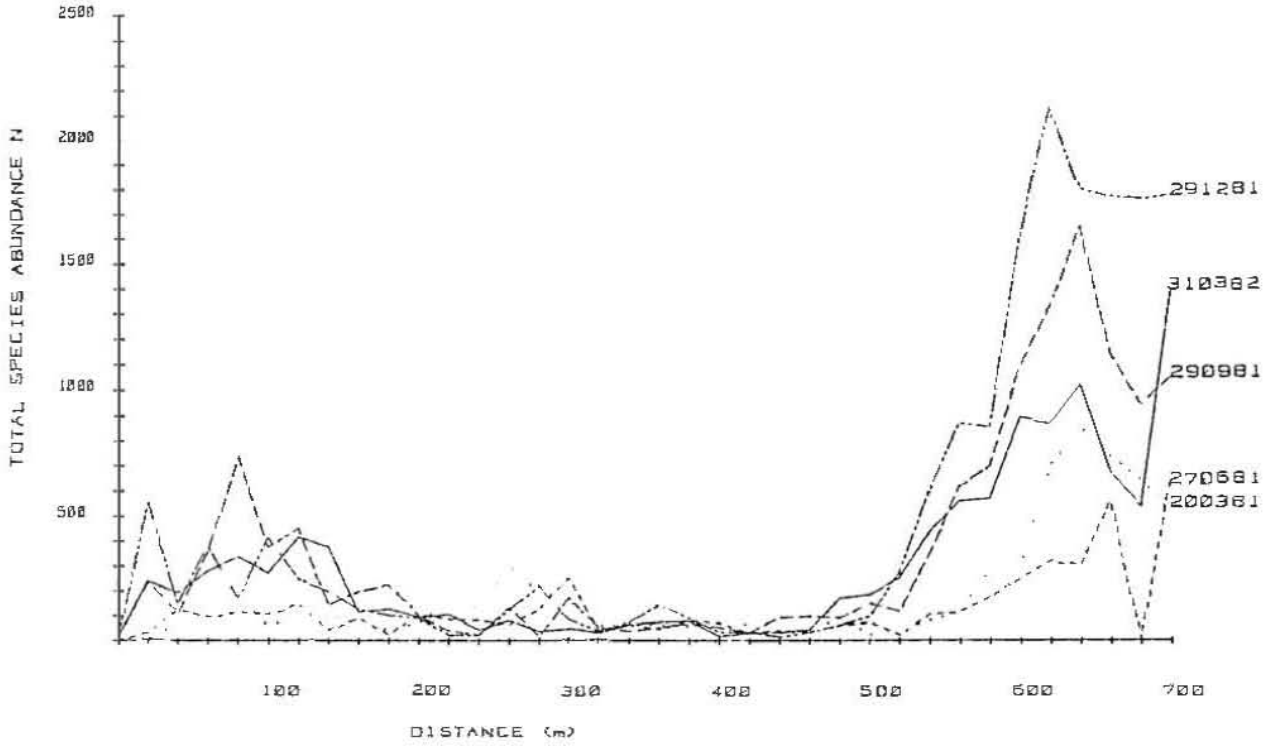


Fig. 4.21(a) Changes in the total *Hydrococcus* abundance along the distribution transects.

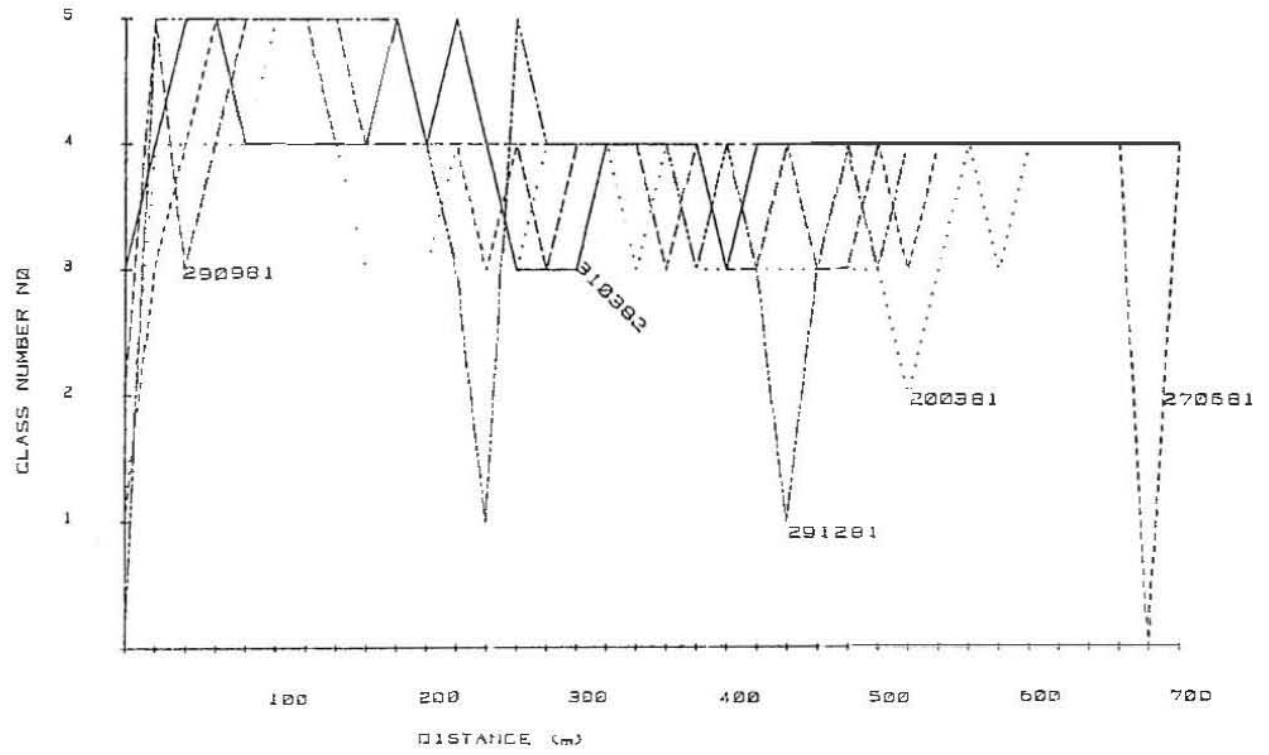


Fig. 4.21(b) Changes in the number of *Hydrococcus* size classes represented along the distribution transects.

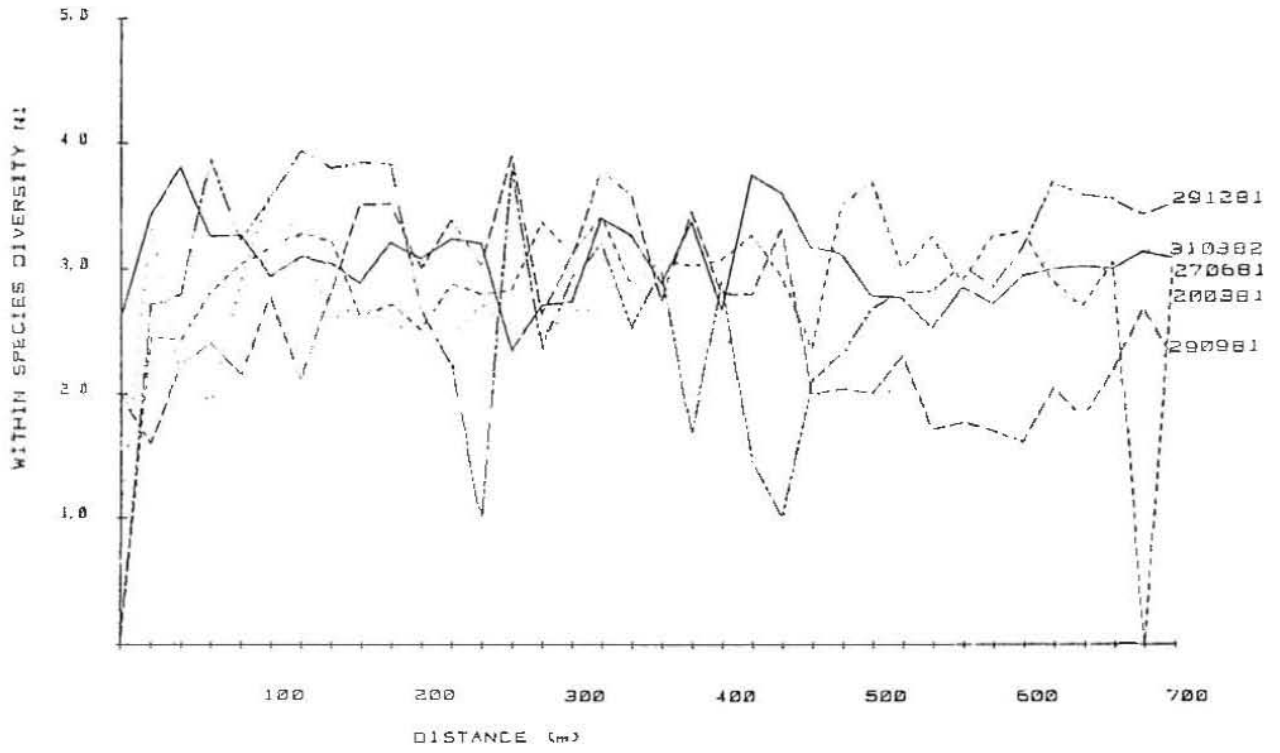


Fig. 4.21(c) Changes in the size class diversity of *Hydrococcus* along the distribution transects.

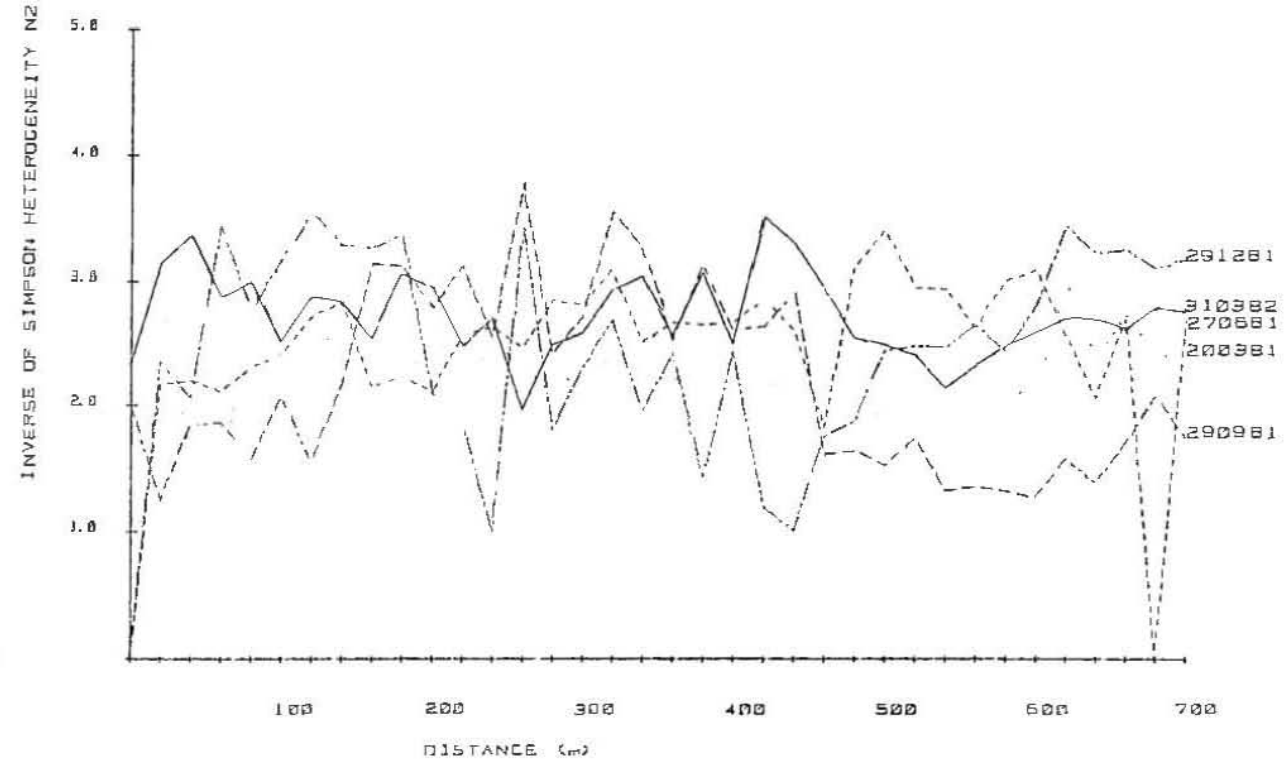


Fig. 4.21(d) Changes in the inverse of *Hydrococcus* size class heterogeneity along the distribution transects.

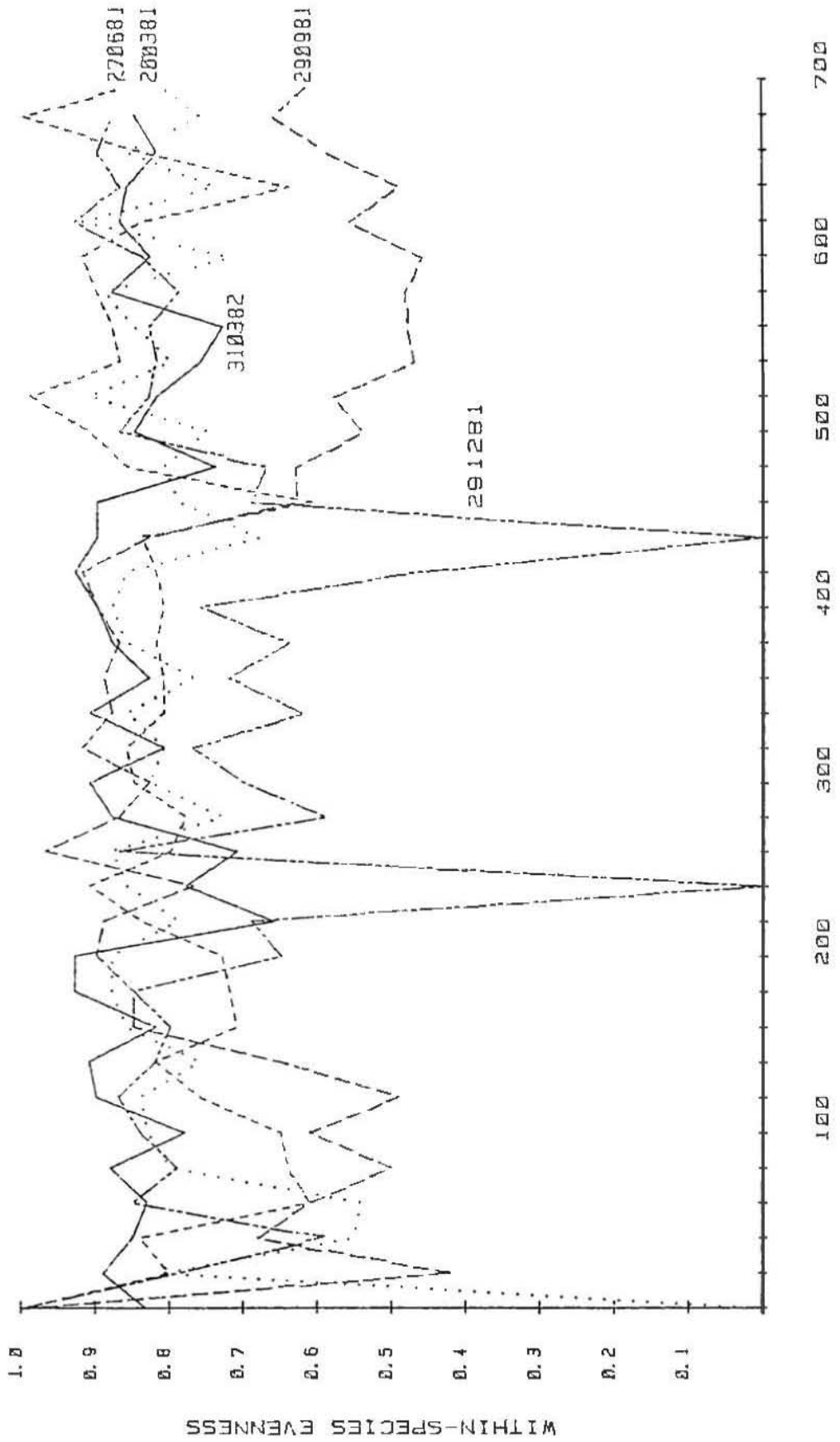


Fig. 4.21(e) Changes in the size class evenness of *Hydrococcus* along the distribution transects.

characteristic of the *Anapella* and *Katelysia* coefficients. This is largely due largely to the consistently high class representation shown by *Hydrococcus* over most of the beach.

Although the overall pattern is for little dependence on beach position, each season has areas of considerable variation. In general, these are less pronounced in the evenness term than in the within-species diversity and heterogeneity terms.

On 200381 the coefficients increase rapidly to reach a maximum near 100 m prior to a slow, steady decline to 400 m and a subsequent slow increase in the lower portion of the beach.

The 270681 pattern is similar over the first 450 m but there is then a sharp increase to a 500 m maximum followed by a slight decline to 700 m.

In spring (290981) there is no 100 m peak. Instead, the coefficients increase steadily to reach a maximum at 300 m and then decline to 700 m; there is a sharp fall after 400 m but from 450 m to 700 m the decline is slight.

The summer (291281) pattern is essentially the same as the autumn and winter patterns but each feature is more exaggerated and the coefficients are more variable. Thus, the 100 m peak is higher and broader and is followed by a sharp fall near 200 m and an equally sharp rise to 250 m. An irregular decline between 250 m and 400 m gives rise to a steep increase between 400 m and 700 m.

The 310382 autumn is similar to the 200381 autumn except for a peak close to 400 m where previously there had been a small trough.

As mentioned, all the above trends are damped considerably in the evenness coefficients.

4.3.2.7 *Zeacumantus* Hill series (Fig. 4.22)

Total *Zeacumantus* abundances are shown in Fig. 4.22(a).

Zeacumantus class representation (Fig. 4.22(b))

Like *Hydrococcus* , *Zeacumantus* has consistently high class representation over most of its distribution zone. The rapid decrease in numbers between 300 m and 400 m is paralleled by a decrease in class number in each season. A small, transient increase in both abundance and class number occurs between 400 m and 500 m. The progressive shift of the abundance curves over the sample period is not reflected in any change in the class representation.

Zeacumantus diversity coefficients (Figs. 4.22(c-e))

There is considerable seasonal variation in the diversity coefficients although three consistent features are apparent. Each season has a peak close to 50 m with a second peak

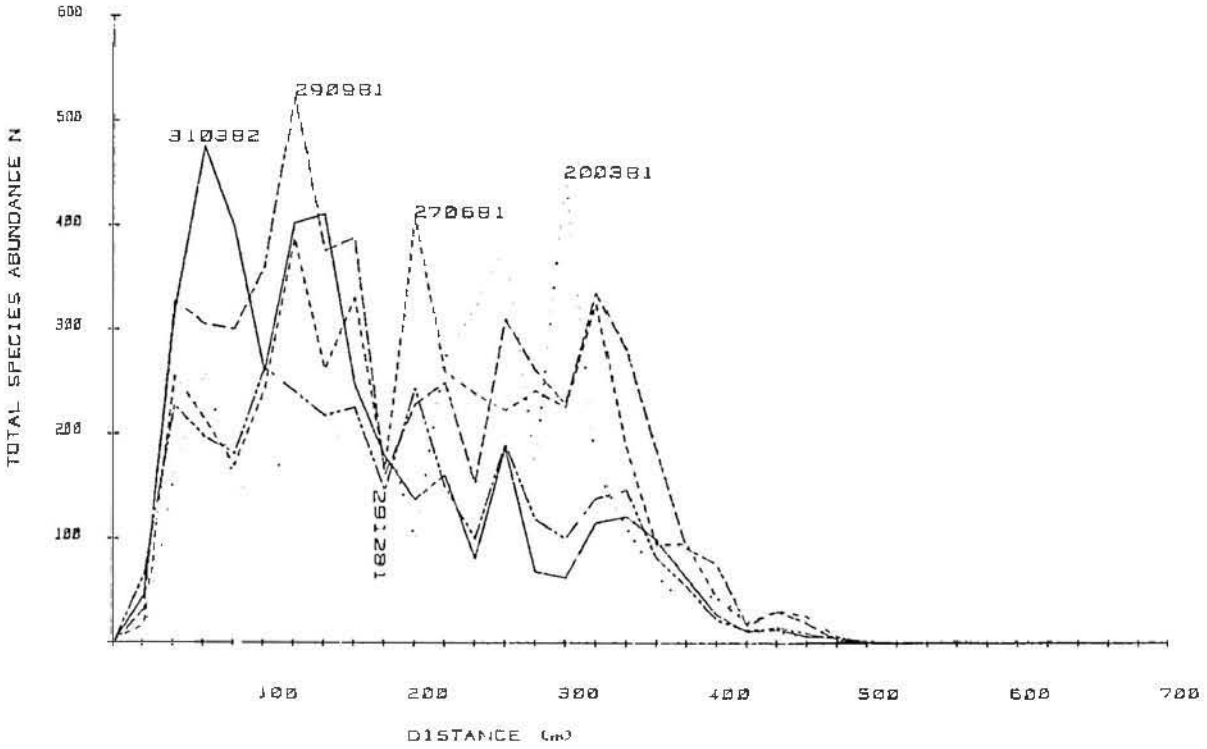


Fig. 4.22(a) Changes in the total *Zeacumantus* abundance along the distribution transects.

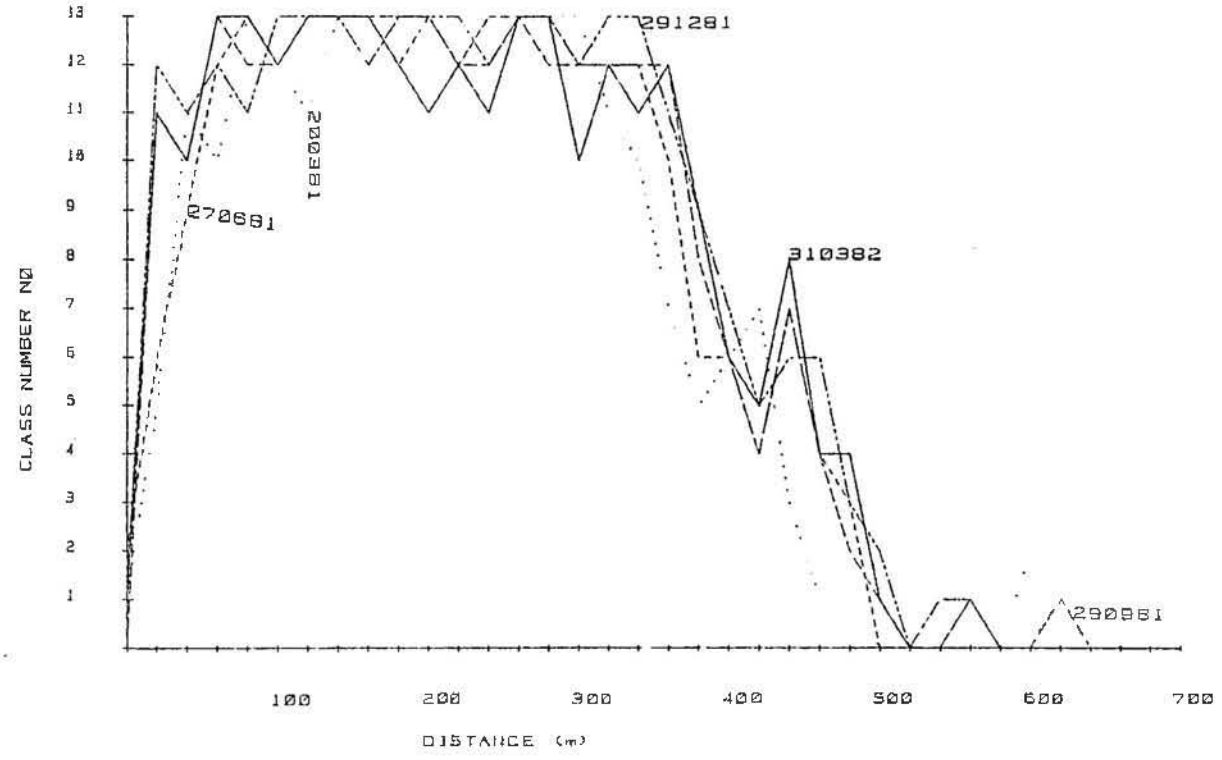


Fig. 4.22(b) Changes in the number of *Zeacumantus* size classes represented along the distribution transects.

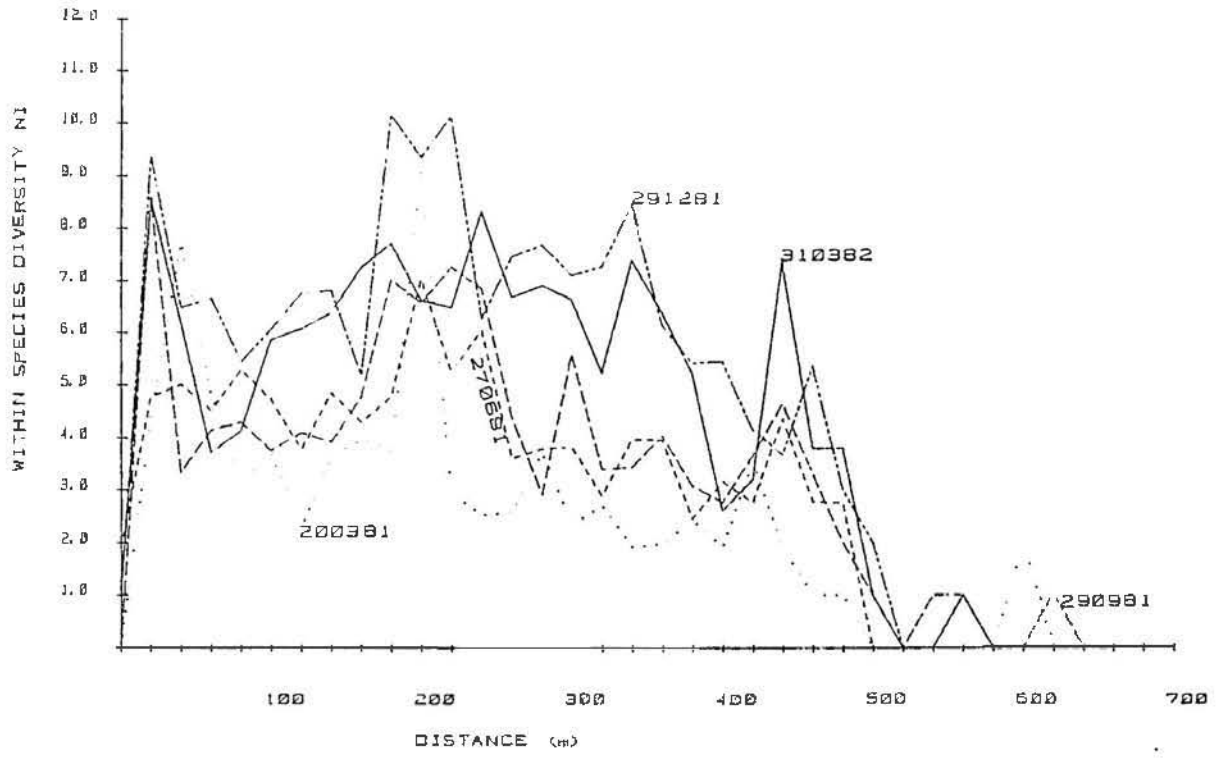


Fig. 4.22(c) Changes in the size class diversity of *Zeacumantus* along the distribution transects.

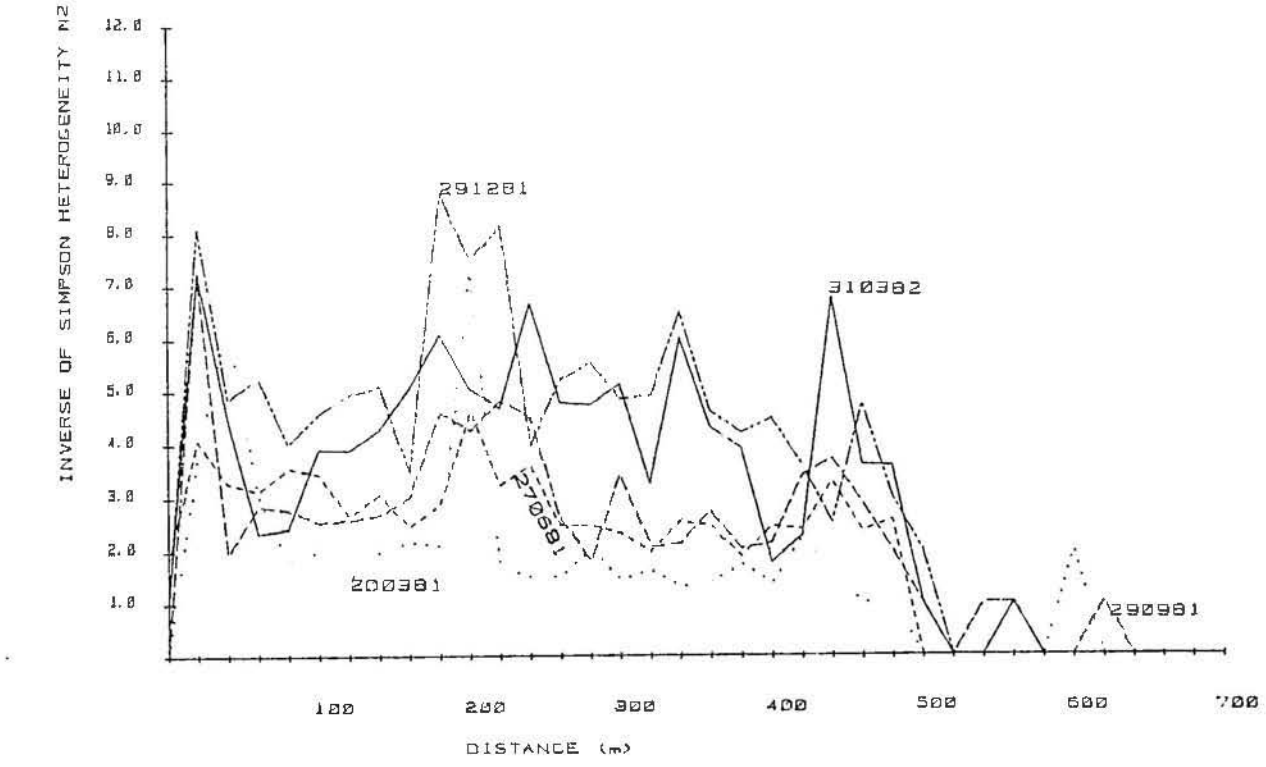


Fig. 4.22(d) Changes in the inverse of *Zeacumantus* size class heterogeneity along the distribution transects.

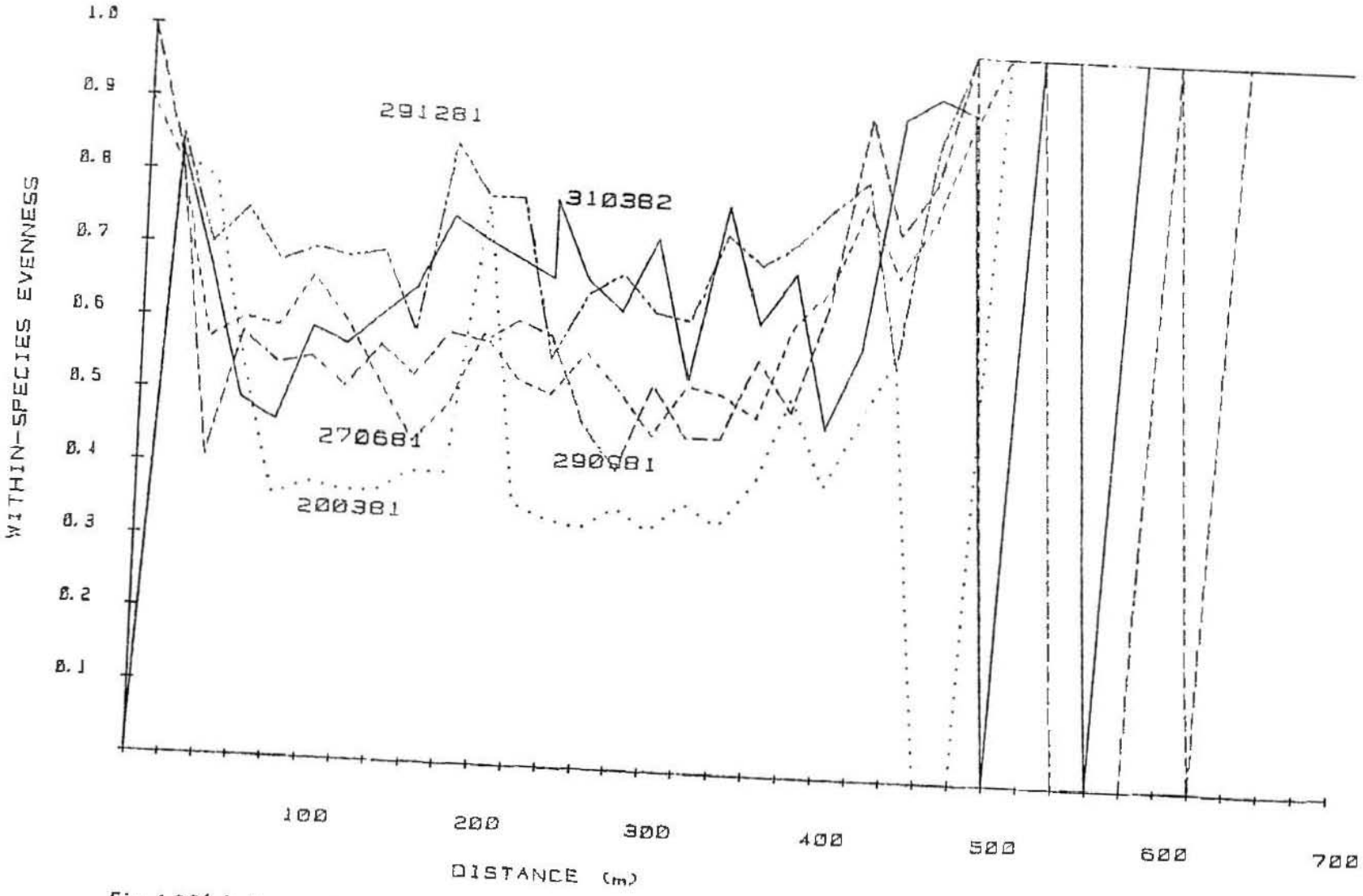


Fig. 4.22(e) Changes in the size class evenness of *Zeacumantus* along the distribution transects.

near 200 m and a smaller peak near 450 m prior to a rapid decline. There is a broadening of the second peak over the sampling period but the first remains well defined. In summer and the following (310382) autumn, the second peak extends down the beach to almost link up with the third peak.

Both the first and third peaks are associated with areas where the *Zeacumantus* abundances are in a state of rapid rise or fall. The sequential changes in the second peak over the sampling period are probably related to the abundances changes over the same period but with the diversity coefficients the effect is a progressive widening of the peak rather than a shifting.

As with *Hydrococcus*, the combination of the within-species diversity and heterogeneity coefficients produces a damping of the above features in the evenness term.

4.3.2.8 *Salinator* **Hill series** (Fig. 4.23)

Total *Salinator* abundances are shown in Fig. 4.23(a).

Salinator class representation (Fig. 4.23(b))

In all seasons, the number of classes represented is highly variable along the transect. There is a general trend, however, for an initial peak near 20 m and then a gradual decline in class number over the first 400 m of the beach with another peak between 500 m and 600 m. There is also a poorly defined peak between 150 m and 250 m. Thus, the seasonal changes in the abundances along the transect are paralleled by changes in the class representation; the seasonal differences is class number are minor, however.

Salinator diversity coefficients (Fig. 4.23(c-e))

The increase in abundance from autumn to spring is accompanied by a decrease in the variability of the diversity coefficients. Both the 150-250 m and 500-700 m abundance peaks are associated with increases in the diversity coefficients. There is no such increase between 0 m and 50 m, however. These patterns are poorly defined in the seasons of low abundance; this is particularly noticeable in the evenness term.

4.3.2.9 *Anthopleura* **Hill series** (Fig. 4.24)

Total *Anthopleura* abundances are shown in Fig. 4.24(a).

Anthopleura class representation (Fig. 4.24(b))

The class number patterns are similar to the abundance patterns, both with respect to position on the beach and season.

Anthopleura diversity coefficients (Figs. 4.24(c-e))

The within-species diversity and heterogeneity coefficients plots are also similar to the abundance plots. In contrast, however, the combination of these coefficients produces very different trends in the evenness coefficient. Apart from the first 100 and last

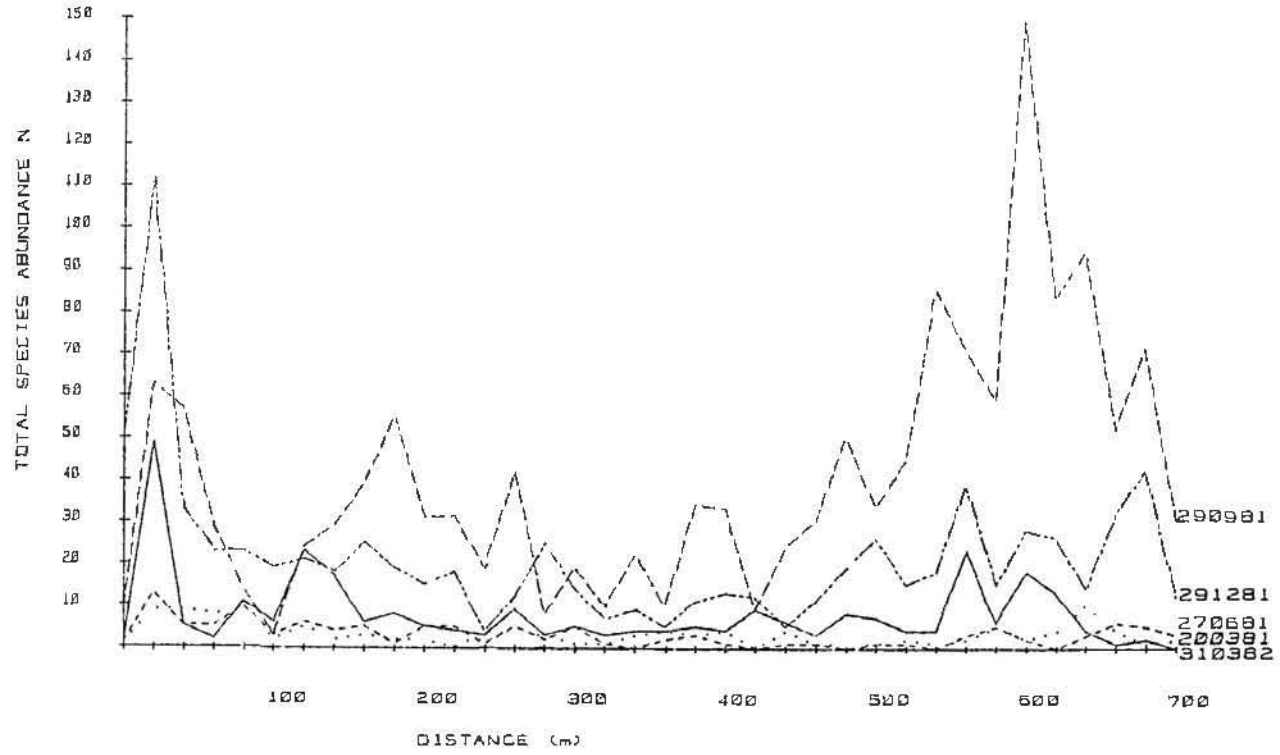


Fig. 4.23(a) Changes in the total *Salinator* abundance along the distribution transects.

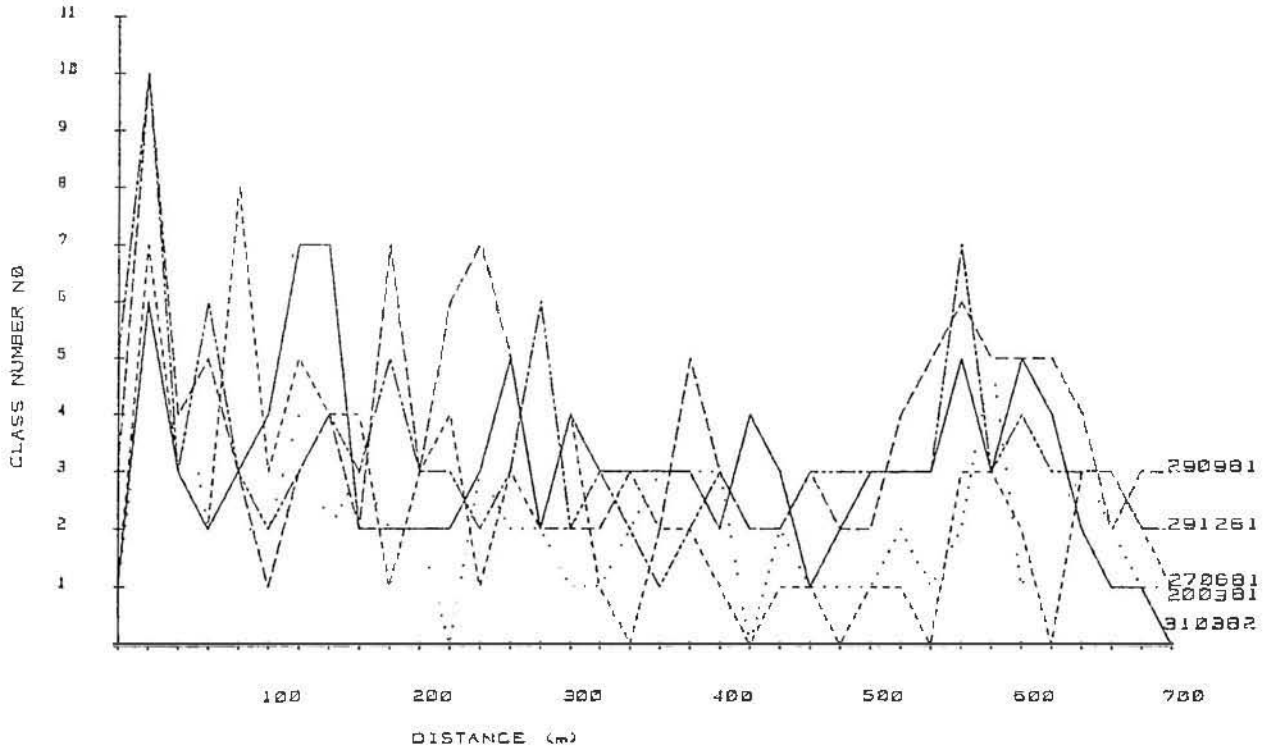


Fig. 4.23(b) Changes in the number of *Salinator* size classes represented along the distribution transects.

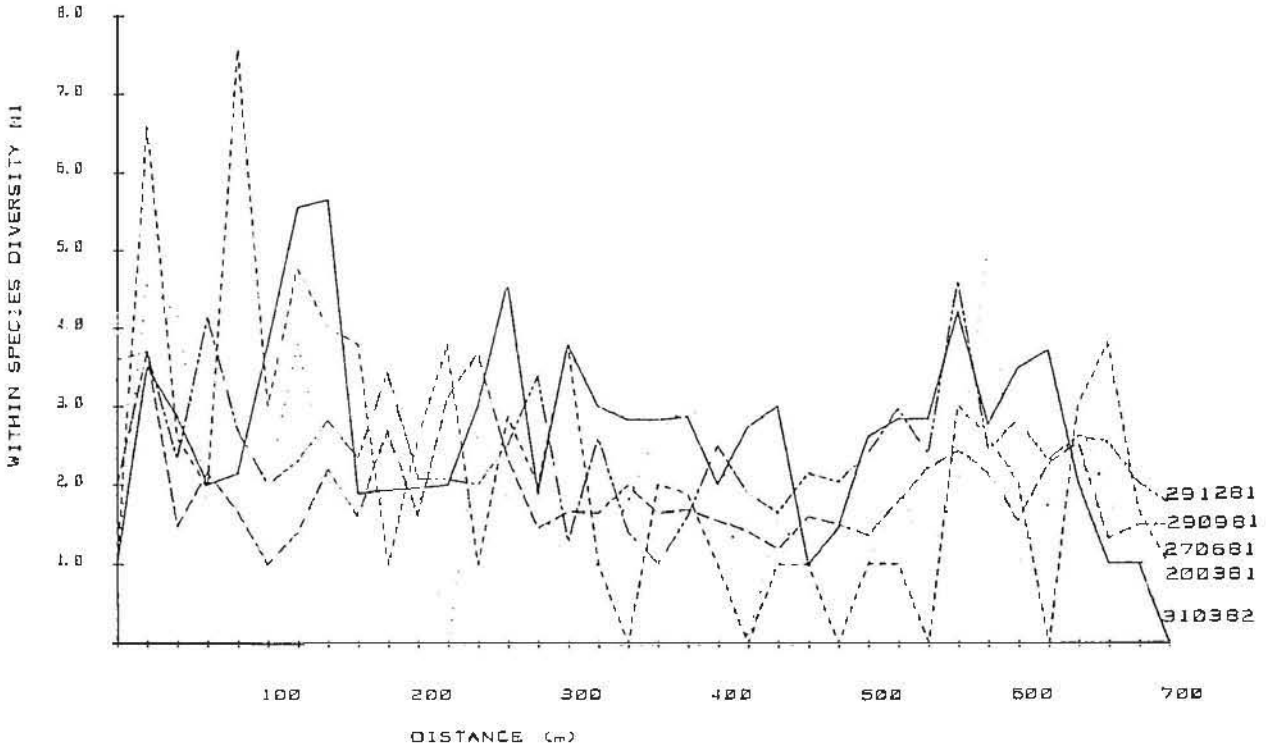


Fig. 4.23(c) Changes in the size class diversity of *Salinator* along the distribution transects.

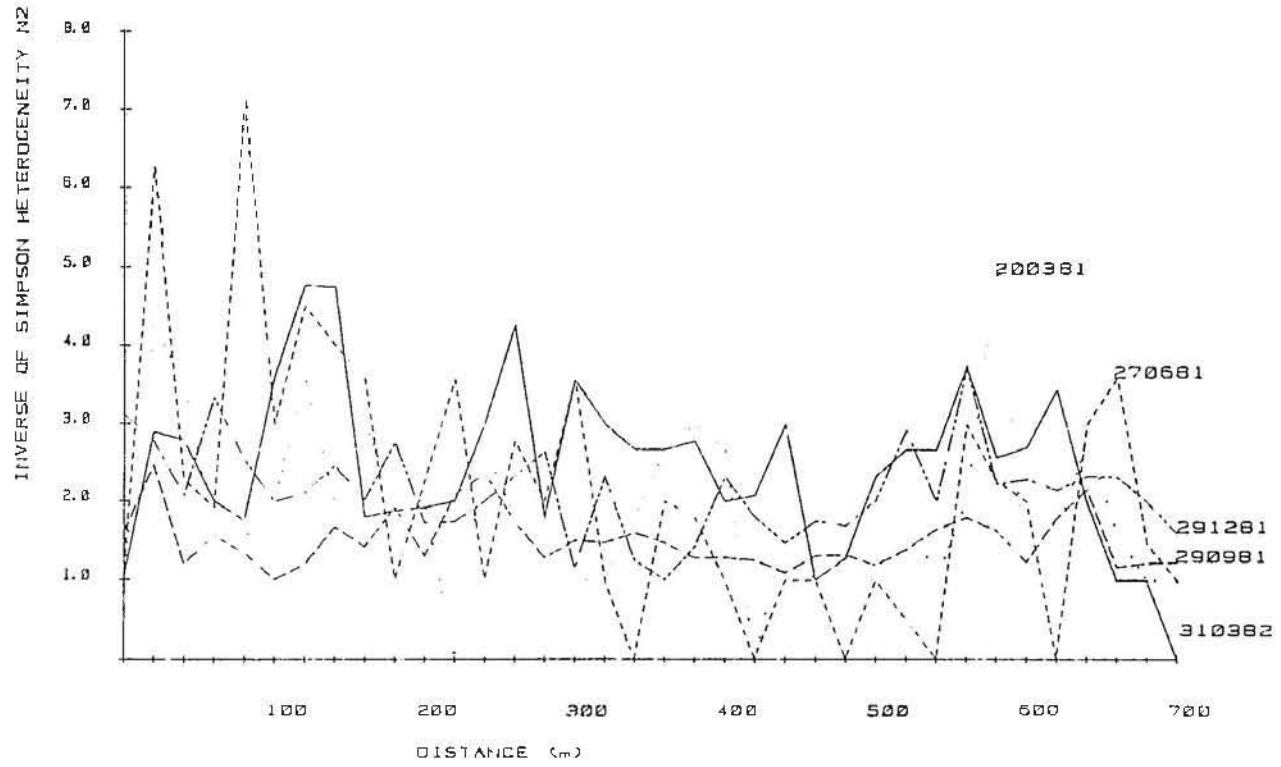


Fig. 4.23(d) Changes in the inverse of *Salinator* size class heterogeneity along the distribution transects.

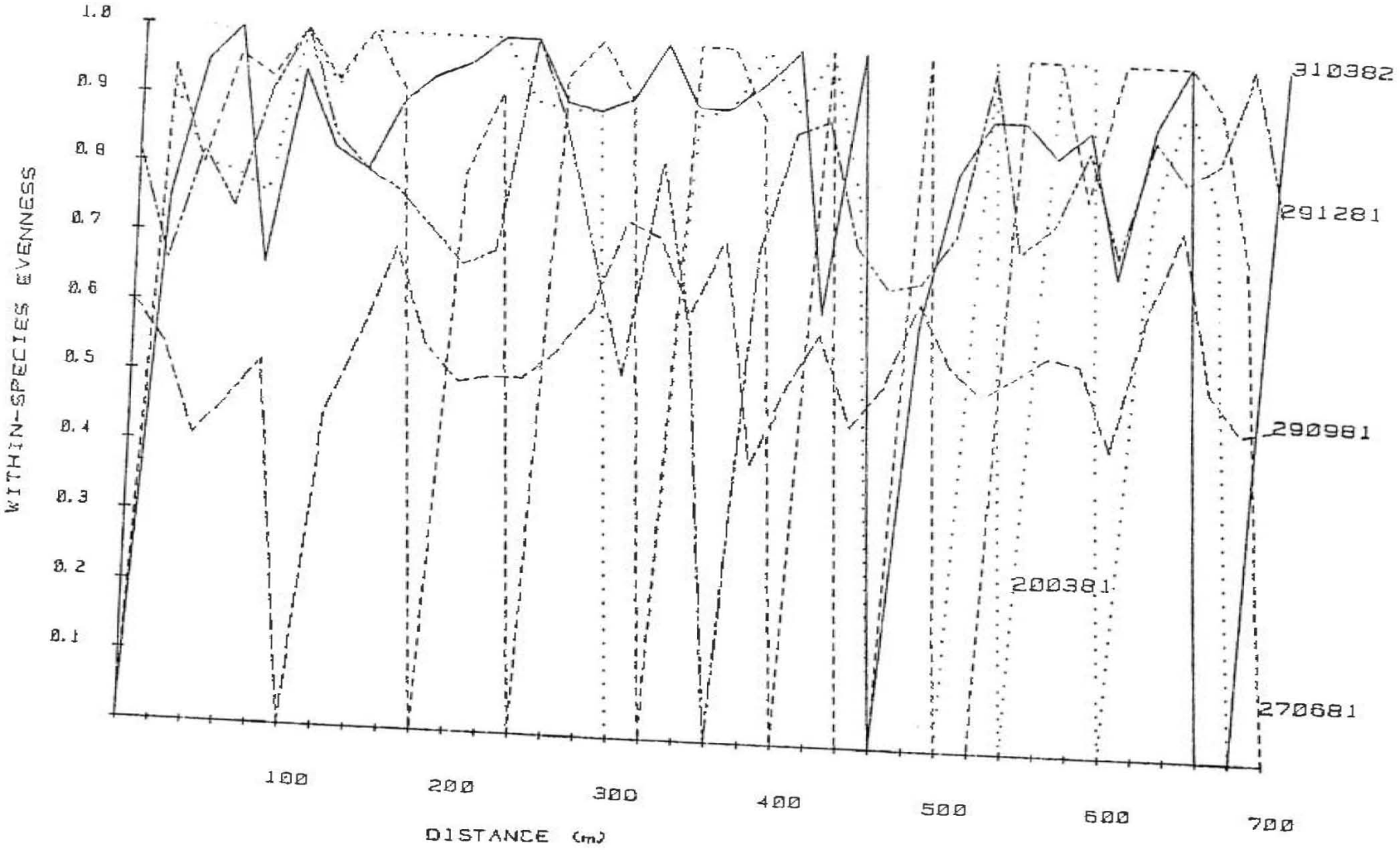


Fig. 4.23(e) Changes in the size class evenness of *Salinator* along the distribution transects.

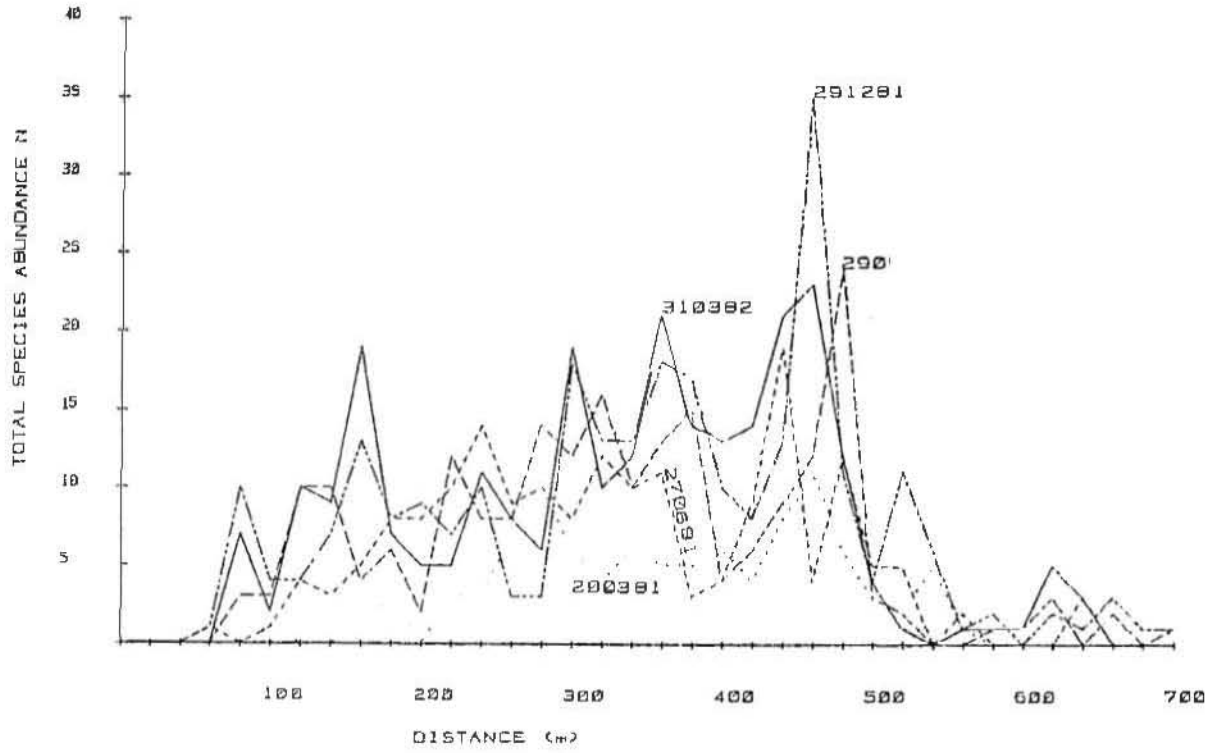


Fig. 4.24(a) Changes in the total *Anthopleura* abundance along the distribution transects.

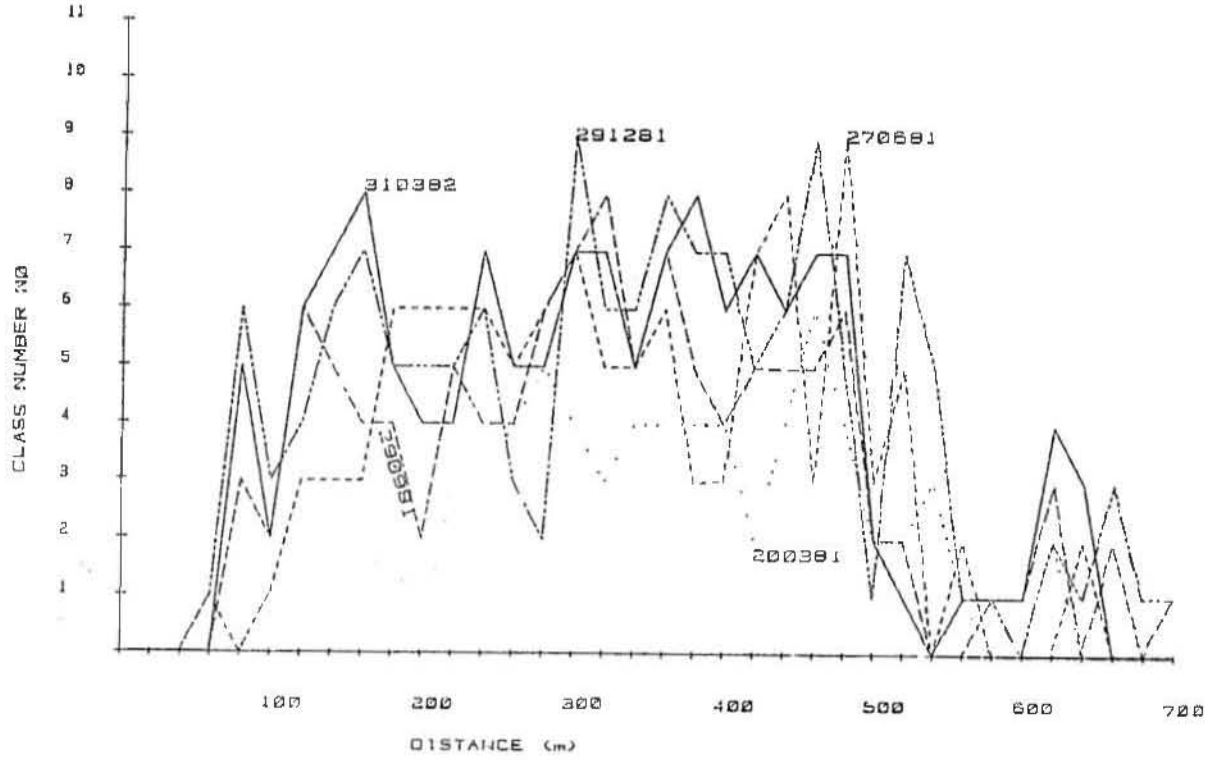


Fig. 4.24(b) Changes in the number of *Anthopleura* size classes represented along the distribution transects.

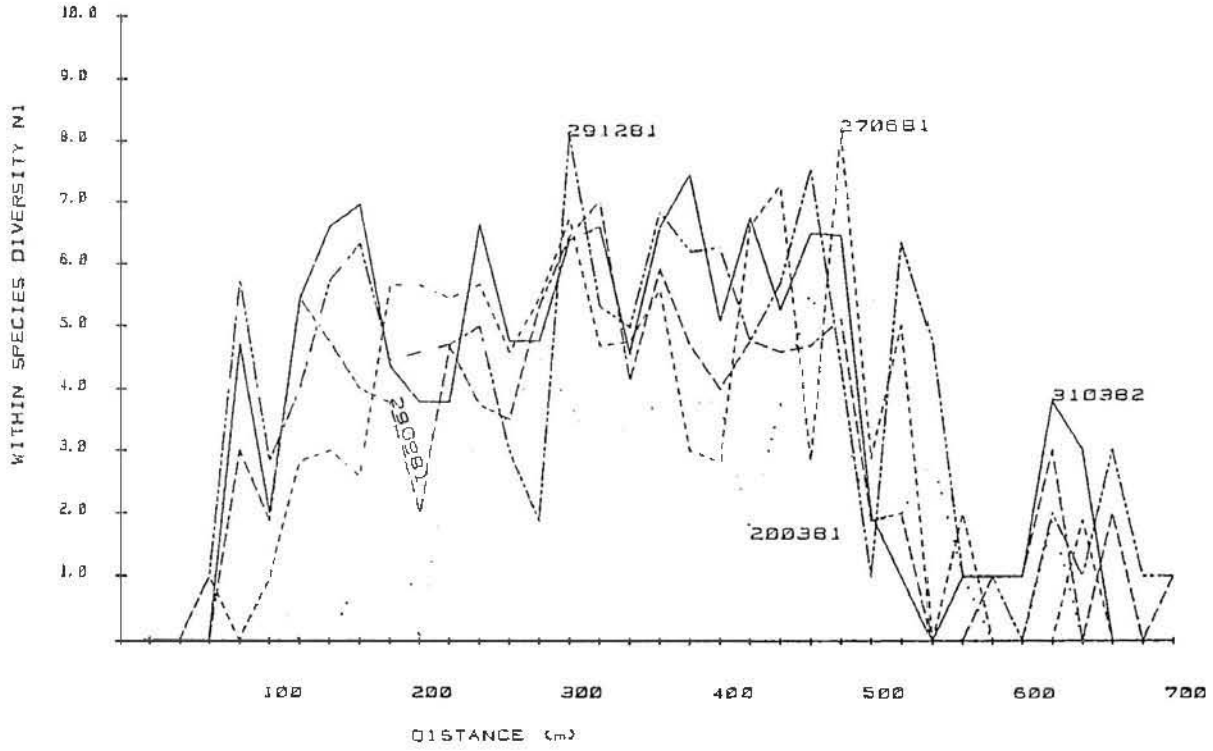


Fig. 4.24(c) Changes in the size class diversity of *Anthopleura* along the distribution transects.

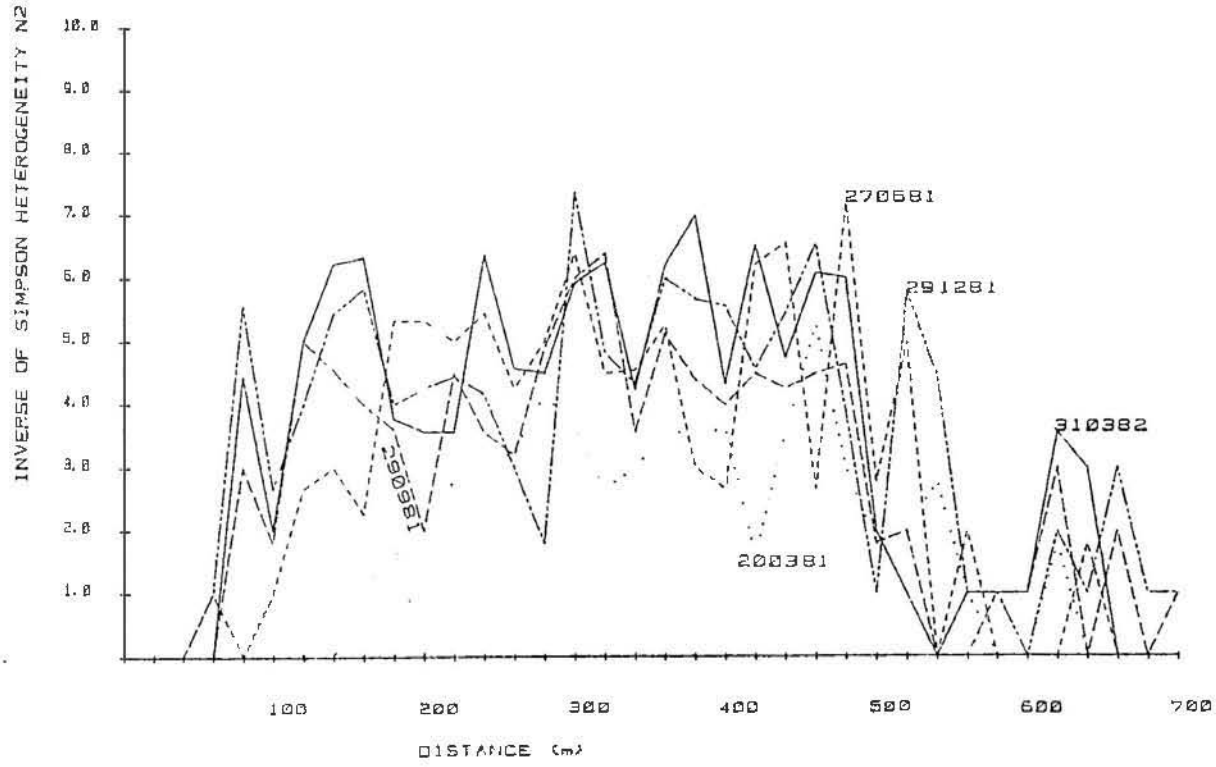


Fig. 4.24(d) Changes in the inverse of *Anthopleura* size class heterogeneity along the distribution transects.

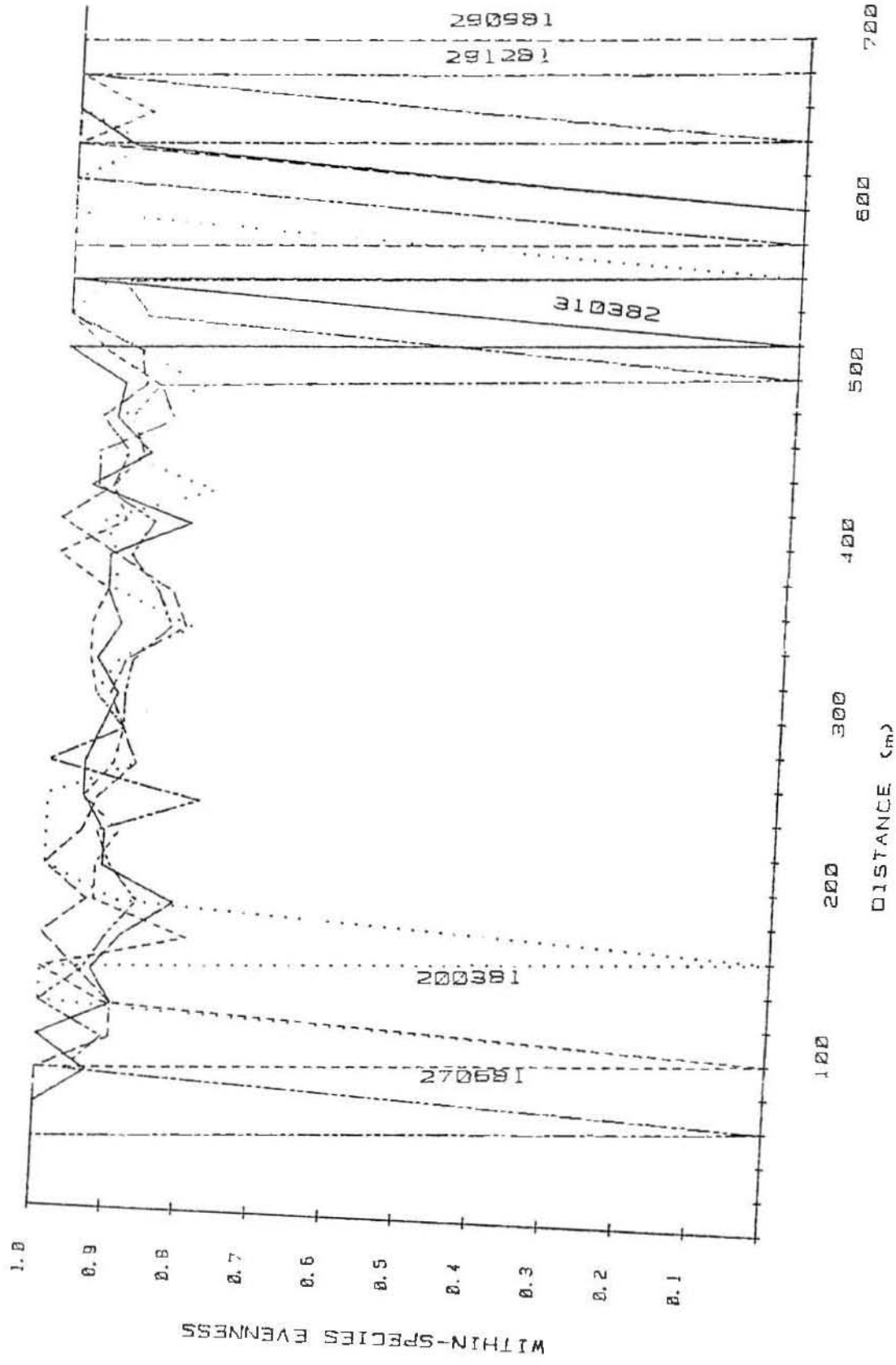
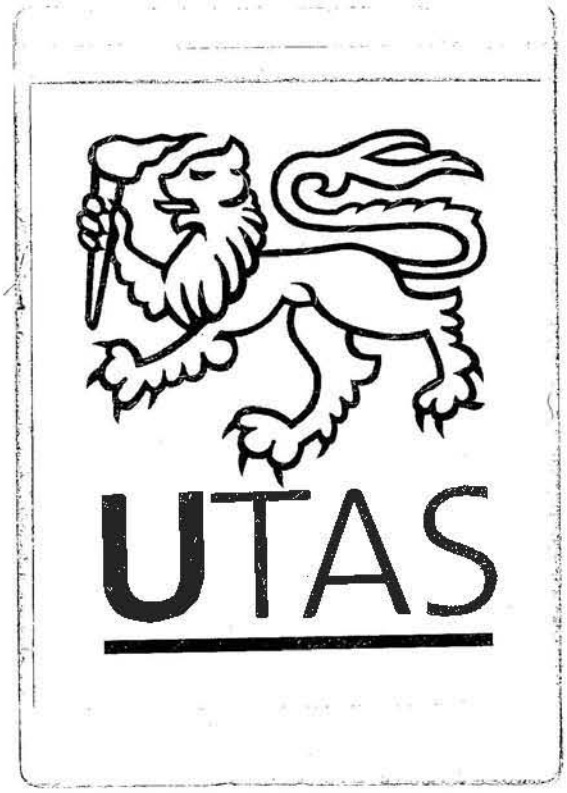


Fig. 4.24(e) Changes in the size class evenness of *Anthopleura* along the distribution transects.

200 m, when it fluctuates meaninglessly, the eveness coefficient remains close to 1.0.



4.4 Discussion

The structure of a biological community will be determined by a complex of biotic and abiotic interactions. An expression of those interactions can be measured by indices of diversity, but it is important to distinguish between the real diversity and the measured diversity. The latter is inevitably dependent on sampling methods and sampling efficiency, and also on the method of calculating the diversity indices themselves. In natural communities it is impossible to consider all biotic and abiotic parameters and any measurement of diversity will necessarily be based on a subset of those parameters.

Typically a decision is taken to include only those organisms collected by a particular sampling procedure and/or only those organisms belonging to a chosen taxonomic group. Similarly, physicochemical parameters are generally selected according to their known or presumed importance in influencing the biology of those organisms. Any interpretation of diversity measures should, therefore, be made with the recognition that a considerable portion of the network of interactions may have been ignored.

In the present study, it is assumed that the selected species and physical parameters represent an unbiased sample of the interaction network and that the observed changes in community structure are therefore a reflection of the general patterns of the entire beach system.

The basic entities of community structure, the species, are also structured (by size classes). Changes in population structure along a tidal gradient have been recorded in many species (Glynn *et al* 1975; Stromgren *et al* 1973; Hamilton 1978; Ansell and Lagardere 1980; Wooldridge 1981; Brown 1982). Such intraspecific zonations may be attributable to a sorting of sizes in the swash or to an active migration of animals to preferred areas (McLachlan 1983). Alternatively, size separation may result from the competitive dominance of larger animals in the search for a resource such as food (Haley 1982).

In a number of species there are changes in population structures associated with the tidal cycle (Turner and Belding 1957; Ansell and Trevallion 1969; Anderson 1971; Trueman 1971; Underwood 1979). Some molluscs have long term migrations along the tidal gradient, including semilunar (McLachlan *et al* 1979) and seasonal (Lambert and Farley 1968; Williams and Ellis 1975; Hamilton 1978; Leber 1982) movements. No attempts were made to examine the possibility of migrations occuring on the Pipe Clay Lagoon tidal flat. The consistency of the seasonal distribution patterns (both within and between species), however, suggests that migrations do not occur.

The two most abundant bivalves, *Anapella* and *Katelysia*, show changes in

population structure which suggest a spatial separation of the two species. *Anapella* and *Katelysia* have approximately mutually exclusive zonations. This is true for both the overall abundances and also for the abundances of similarly sized animals. Spatial segregation between two bivalves has been recorded several times (Rapson 1952; Ansell *et al* 1972; Peterson 1977; McLachlan 1980) and is usually interpreted as being a reflection of competition for space (Peterson 1977). The three dimensional plots of the population structures of *Anapella* and *Katelysia* fit together much like a three dimensional jigsaw, indicating a well established and well maintained separation.

There are indications that *Wallucina* and, to a lesser extent, *Soletellina* reach their highest densities near, or below, the zone 5 beach ridge, where the total abundances *Anapella* and *Katelysia* are lowest. It appears, then, that all bivalves tend to be segregated in space on the tidal flat. *Soletellina* shows the weakest segregation and this could be attributable to its different mode of feeding (deposit) compared to the other bivalves (suspension).

The deposit feeding gastropods, *Hydrococcus* and *Salinator*, are both distributed over most of the tidal flat. In contrast to the bivalves, neither species shows evidence of strong intraspecific zonation. In both species, abundance peaks occur at either end of the transects. Generally, the major abundance peaks do not appear to be mutually exclusive. With the smaller abundance fluctuations, however, *Hydrococcus* and *Salinator* often exhibit opposite trends; for example, a *Hydrococcus* peak near the top of the spring beach coincides with a *Salinator* trough.

Hydrococcus and *Salinator* do show a spatial separation among similarly sized animals. When one or both species reaches high densities, however, this separation is not noticable, suggesting that other factors are of prime importance in determining the relative abundance of the two species. Levinton (1979) reviewed the work on resource limitation in deposit feeders, noting that the distributions of deposit feeders are influenced by detrital influx, microbial production and space. The latter incorporates the two former resources and a segregation in space may simply be a reflection of a segregated trophic resource.

Neither *Hydrococcus* nor *Salinator* show segregation with the deposit feeding bivalve, *Soletellina*, but the low numbers of the latter species may obscure any trends. Both gastropods, however, reach their highest abundances in areas of the beach where there are low numbers of large *Anapella* and *Katelysia*. These observations support the trophic group amensalism hypothesis of Rhoads and Young (1970). According to this hypothesis, sediment reworking by deposit feeders produces a faecal rich substrate

surface that is easily resuspended. This can inhibit populations of suspension feeders, either by clogging their filtering structures, burying newly settled larvae, discouraging settlment of larvae or preventing the attachment of sessile epifauna. The destabilising of substrates is largely restricted to deep, subtidal bottoms because of the stabilising actions of structures such as seagrasses, algal mats and worm tubes in shallow waters (Rhoads 1974).

There has been considerable support for the amensalism hypothesis (Bloom *et al* 1972; Aller and Dodge 1974; Peterson 1977; Whitlach 1980) and it seems to apply principally to bivalves in muddy sediments. Meyers (1977), however, has shown that trophic group amensalism can operate in a clean, sandy environment. Also, Brenchley (1981) found that it applied to other animal groups and he suggested a need to shift the emphasis from trophic group to relative mobility in the bioturbation hypothesis.

In Pipe Clay Lagoon it appears that the settlment of bivalve larvae is independent of the densities of deposit feeding gastropods. The survival of settled larvae, however, probably depends partly on the abundances of *Hydrococcus* and *Salinator*. Where those gastropods are most abundant, the mortality of juvenile bivalves appears to be greatest and this may ultimately lead to the spatial segregation of the deposit and suspension feeders. Migration and passive resettlement may also play a role but these factors were not examined in this study.

Among the herbivorous gastropods, *Zeacumantus*, *Rissopsis*, *Microdiscula* and *Bembicium* are all common in the top half of the beach. *Zeacumantus* has a very stable population structure with respect to both time and space. At either end of its zone there are sharp decreases in abundances. Over the first 40 m of the transect, where there are comparatively low numbers of *Zeacumantus*, *Bembicium* reaches its greatest densities, suggesting a spatial segregation between the two species. The densities of *Rissopsis* are variable over time. In those seasons where the *Rissopsis* populations show well defined structures, there is some evidence that *Rissopsis* densities peak (close to the 200 m station) where is a slight decline in *Zeacumantus* densities. Any hypothesis of spatial segregation between *Zeacumantus* and *Rissopsis*, however, must remain tentative. Also, the occurrence of *Microdiscula* in the transect samples was too irregular to allow any firm conclusions to de drawn.

Austrocochlea and *Notoacmea* are comparatively uncommon and both appear to be most numerous in the lower half of the beach. This is unlikely to be due to a simple relationship with immersion time because they are also common on rocky outcrops high on the beach (away from the transect). Much of the similarity of the distributions of these species can be attributed to the frequent use by *Notoacmea* of *Austrocochlea* as a

substrate. Both species are more typical of hard substrate habitats and would be less efficient feeders than the other herbivorous gastropods in soft sediments. This could account for their general absence from the upper half of the beach.

As with the deposit feeders, the spatial segregation of the herbivorous gastropods probably reflects an underlying segregation based on the availability of food resources (mainly microalgae).

The distribution of the carnivorous molluscs would be expected to parallel those of their prey or hosts. Both *Nassarius* and *Agatha* are more abundant in the middle reaches of the beach, suggesting *Anapella* is the main source of food for both. *Cylichnina* shows distribution patterns similar to those of *Hydrococcus* juveniles, which are a likely food source. The anenome, *Anthopleura* , is dependent on large *Anapella* and *Katelysia* for substrates and shows a similar distribution to those animals. Predation by *Anthopleura* may be partly responsible for the reduction in *Hydrococcus* (and, to a lesser extent, *Salinator*) numbers in those sections of the beach.

On the basis of the above observations, it is possible to construct a hypothesis for the role of biotic interactions in maintaining the community structure of Pipe Clay Lagoon:

Working hypothesis for the maintenance of the community structure

The deposit feeding gastropods, *Hydrococus* and *Salinator* , can tolerate a wide range of conditions and are distributed over most of the beach and possibly compete for trophic resources. Their feeding activities rework the substrate, making the sediment-water interface unstable. *Soletellina* is also a deposit feeder but appears to be intolerant of exposure and is confined to the lower sections of the beach.

Anapella and *Katelysia* larvae settle indiscriminantly on the substrate but are unable to survive in areas of highly reworked sediment. In those areas where there are relatively low densities of deposit feeders, the bivalves are able to survive to maturity. Competition for space between large *Anapella* and *Katelysia* leads to a segregation of the two species along the tidal gradient. *Katelysia* , being less tolerant of dessication becomes confined to the lower sections of the beach.

Wallucina is able take advantage of low *Anapella* and *Katelysia* numbers near the 500 m beach ridge and reaches its highest densities there.

Anthopleura uses large bivalves as a substrate and is most abundant

in the middle sections of the beach. Passive predation by *Anthopleura* may act to keep the numbers of deposit feeding gastropods low, thus minimising the effects of the trophic group amensalism.

The upper half of the beach appears to be most suitable for gastropods feeding on microalgae. The distribution of deposit feeders and microalgae feeders are apparently independent. Competition for food resources leads to a spatial segregation of *Zeacumantus* and *Bembicium*. *Bembicium*, being more tolerant of exposure and possibly less efficient at feeding than *Zeacumantus*, forms an abundance zone at the extreme top of the beach. Less common herbivorous gastropods (*Rissopsis* and *Microdiscula*) take advantage of irregular reductions in *Zeacumantus* densities and are most common where those reductions occur. *Austrocochlea* and *Notoacmea* are likely to be relatively inefficient feeders in soft substates and are excluded from the upper sections of the beach.

Nassarius appears to obtain is main food supply by scavenging dead, and preying on living, *Anapella* and *Katelysia* and is therefore most abundant in the middle reaches of the beach. *Agatha* is probably host specific on *Anapella* and has a similar distribution. *Cylichnina* is likely to prey on juvenile *Hydrococcus* and has a similar distribution to that species. Thus, the distribution of predators is determined by the distribution of prey and not *vice versa*.

The variability of benthic communities appears to be influenced by the substrate characteristics, with temporal variability being greater in mud sediments than in more stable sand sediments (Eagle 1973). In Pipe Clay Lagoon the population structures, and consequently the overall community structure, show a high degree of consistency over time. The lagoon beach is particularly stable, as evidenced by the minimal variations in beach profile, and the community appears to reflect this.

Peterson (1977) made similar observations of a lagoon community. He noted a pattern of depth stratification among the species (where there was vertical overlap there was horizontal separation) and a nearly constant community composition. He also concluded that competition for space was probably the most important factor in maintaining the community consistency.

The lagoon community's characteristics allow an examination of the relationships between competition and diversity in the effective absence of large-scale disturbance and

predation.

Apart from the extreme upper part of the beach, the number of species represented in the samples remains relatively constant throughout the beach, other than small, positive deviations near the beach ridges. Diversity and evenness closely parallel one another and below 200 m are approximate mirror images of the overall community abundance. Above 200 m the diversity and evenness terms remain high despite a reduction in abundance. This is due to a simultaneous reduction in species number.

Most of the abundance changes are due to fluctuating densities of juvenile *Anapella*, *Katelysia* and *Hydrococcus* and are largely determined by the beach topography. When all 0 mm animals are excluded from the analysis, quite different abundance, diversity and evenness patterns emerge. The species representation remains virtually the same but the central sections of the beach appear relatively depauperate. Diversity and evenness remain fairly constant in the top half of the beach but there is a marked increase in diversity (not evenness) near the 400 m station. Below this, both diversity and evenness decline. Generally, the exclusion of juveniles from the analysis decouples those indices from the abundance term.

The trends in diversity are similar to those that could be predicted from both the dynamic equilibrium (Huston 1979) and intermediate disturbance (Connell 1978) hypotheses. The latter, however, is applicable to communities where the rate of population reduction through disturbance is much faster than the recovery rate of those populations; disturbance appears to be a negligible factor in Pipe Clay Lagoon.

Increasing intensity of competition should lead to a reduction in species evenness and ultimately species number (Huston 1979). Diversity, therefore, should vary inversely with competition intensity (Levins 1968; Vandermeer 1970; Huston 1979). According to Huston's (1979) general hypothesis, competitive displacement of species, rather than differences in competitive abilities, is the mechanism by which diversity is controlled. In Pipe Clay Lagoon it appears that the rates of competitive displacement are highest in the top and bottom sections of the beach, due mainly to trophic group amensalism.

The diversity trends calculated in the presence and absence of 0 mm animals can be respectively regarded as the before and after of competitive displacement. Prior to displacement, diversity is simply a function of overall abundance, which in turn is largely determined by the physical characteristics of the beach. In that case, diversity cannot be interpreted as a product of biotic interactions. After displacement, however, the diversity patterns are probably a product of those interactions.

Species diversity in shallow waters has usually been shown to be a positive function of

depth (Stromgren *et al* 1973; Chelazzi and Vannini 1980; Femino and Mathieson 1980; Flint and Holland 1980) and/or substrate complexity (Boesch 1973; Kohn and Nybakken 1975; Kohn and Leviten 1976; Luckhurst and Luckhurst 1978; Chelazzi and Vannini 1980; Flint and Holland 1980). Disturbance has also been implicated (Lieberman *et al* 1979; Sousa 1979) and may control diversity as predicted by the intermediate disturbance hypothesis (Connell 1978).

Biotic interactions, such as predation (Reise 1978; Peterson 1979; Wiltse 1980) and grazing (Lubchenco 1978), have been found to influence the diversity of shallow water, soft sediment communities but there appear to be no previous shallow water studies that support the dynamic equilibrium hypothesis.

There also appear to have been no studies that have followed changes in hierarchical diversity and/or within-species diversity along an environmental gradient. The biological significance of these indices is difficult to interpret but they make a useful comparison with the species diversity indices. Although the hierarchical abundance (overall class number) patterns are different to the species number patterns (particularly in the lower half of the beach), hierarchical diversity and evenness are similar to their individual abundance counterparts, when 0 mm animals are included; similar causative arguments can be applied to both.

The trends in class number for *Anapella* and *Katelysia* are approximately mutually exclusive, as indicated by the distribution transect size frequency plots. These further illustrate the spatial segregation of the two species. *Anapella* within-species diversity increases in areas of trophic group amensalism. The reductions in diversity are largely due to the decrease in numerical dominance by juveniles. In contrast, major increases in *Katelysia* within-species diversity occur on the 500 m beach ridge, although these are again due to decreases in juvenile dominance. The *Katelysia* juveniles appear to have a greater susceptibility to exposure, relative to their susceptibility to trophic amensalism; with *Anapella*, the opposite is true.

The deposit feeding gastropods, *Hydrococcus* and *Salinator*, show little consistent trend in diversity indices along the distribution transects. This probably reflects their comparative insensitivity to physical and biotic interactions. Both species show the greatest class representation near the top of the beach, mainly because of the relative abundance of large animals there.

The within-species diversity of *Zeacumantus* approximately parallels the overall abundance of that species. Class representation is maximal throughout most of its zone and individuals are distributed among those classes with consistent evenness. At either end of

the *Zeacumantus* zone, evenness increases as fewer classes are represented. The population structures appear to be independent of those of other species.

Similarly, *Anthopleura* diversity trends parallel the trends in overall *Anthopleura* abundance. Both abundance and diversity have a parabolic shape, decreasing at either end of the *Anthopleura* zone. Evenness, however, remains high and constant throughout the zone and reflects the stable population structure of that species.

The within-species diversity patterns, then, also fit with the mechanisms suggested to be responsible for the maintainance of the community structure of Pipe Clay Lagoon.

The spatial segregation producing the community structure may have both active and historical components. This possibility is examined in the following chapters.

CHAPTER 5

ONE-DIMENSIONAL SPATIAL INTERACTIONS AMONG SPECIES AND ABIOTIC AND BIOTIC DETERMINANTS OF ZONATION PATTERNS

5.1 Introduction

Seasonal and spatial variations in the structure of the Pipe Clay Lagoon community, and its constituent populations, have been described in previous chapters. In this chapter, the roles of abiotic and biotic factors in controlling those structures are examined.

The intertidal zones of soft and hard shore environments typically show a zonation of organisms along the tidal gradient. There have been numerous attempts to develop general descriptions and theories of zonation patterns. Stephenson and Stephenson (1949) described general features of rocky shore zonation in terms of exposure and faunal types. Dahl (1952) suggested a similar universal scheme for the zonation of sandy beaches.

Both schemes describe exposure-related zonation patterns that can be attributed to the relative importance of aerial/aquatic respiration, resistance to desiccation and tolerance of temperature and salinity fluctuations. Exposure has been shown to be an overriding factor in many intertidal communities (Doty 1946; Doty and Archer 1950; Hughes and Thomas 1971; Vohra 1972; Wieser and Schiemer 1977) and zonation of intertidal organisms can be induced by exposure in tidal machines (Townsend and Lawson 1972; Underwood 1972 a, b; Carefoot 1981). Exposure is less important in soft sediments because animals are able to burrow into the substrate and so restrict moisture loss (Meadows 1964; Johnson 1965; Seapy and Kitting 1978; Holanov and Hendrickson 1980).

The schemes of Stephenson and Stephenson (1949) and Dahl (1952) have proved to be useful generalisations, but both are descriptive and make little attempt to identify causes of the observed zonations. Connell (1970, 1972) and Paine (1974) were among the first to discuss possible causal factors of zonation on rocky shores. Earlier, Salvat (1964 , cited by Bally 1983) proposed a causal sheme for intertidal beaches that was based on the interstitial hydrodynamic conditions of the beach. Salvat recognised four zones: the zone of dry sand, above neap tides; the zone of water retention, where water loss is due to gravity and some water is retained in the interstitial spaces; the zone of resurgence, with intensive circulation of interstitial water during both high and low

tides, and the zone of saturation, where the sediments are permanently saturated. Pollock and Hummon (1971) supported these zones and also suggested further subdivisions.

The microfauna and meiofauna, in particular, are dependent on the interstitial habitat characteristics, and their abundance is determined principally by the interstitial water content, water circulation and oxygen availability (Jansson 1967; Brown 1983). The deposit feeding macrofauna also show correlations with sediment type and these associations can often be related to the availability of food between, and on the surface of, the sediment particles (Driscoll 1975; Fenchel 1975; Grange 1977; Whitlach 1980).

The distribution and abundance of many benthic organisms have been shown to correlated with grain size (Dale 1974; Grange 1977; Warwick and Davies 1977; Seapy and Kitting 1978; Wells 1978; Tunberg 1981) and this has frequently been attributed to the size of the interstitial spaces within those sediments. Hulings and Gray (1976), however, found that poorly sorted sediments had smaller pore spaces for a given median grain size, and therefore a reduced interstitial population; they suggested that sorting may be more important than grain size in controlling the interstitial biota.

There may be positive feedback relationships between deposit feeders and the microbial food species. Bioturbation and faecal production by deposit feeders increases the surface area and food supply available to the microfauna which, in turn, results in an increased food supply for the deposit feeders (Driscoll 1975; Levinton *et al* 1978). The increased food supply can allow a greater number of deposit feeding species to coexist (Whitlach 1980). Such feedback mechanisms do not always exist, however (Pace *et al* 1979). When food becomes limiting for deposit feeders, there may be intra- and interspecific resource partitioning, often according to preferred grain size of the sediment, and this can lead to a spatial separation of faunal groups (Watling 1975; Fenchel and Kofoed 1976; Grange 1977; Whitlach 1980).

Filter feeders may also compete for limited resources. In the intertidal zone, access to food rather than food availability is often the critical factor for filter feeders and competition is for space to obtain food (Green and Hobson 1970; Peterson 1977). Again, this competition may lead to a spatial segregation of species (Ansell *et al* 1972; Peterson 1977).

Segregation also occurs within resources other than food. Fenchel (1978) recognises habitat niches and time niches, in addition to food niches, in soft intertidal substrates. Coexistence of competing species can be facilitated by behavioural patterns which segregate those resources (Spight 1981). Mobile species, for example, often show tidal migrations, allowing for more efficient utilisation of limiting resources (Zann 1973;

Chelazzi *et al* 1983; Gianuca 1983). Sedentary suspension feeders may show segregation according to depth within the sediment (Peterson and Andre 1980).

Competition between conspecifics has been found to account for spatial changes in population structures. Vermeij (1972) noted that rocky shore intertidal gastropods generally show increases in body size up the beach in littoral fringe species, and decreases in body size up the shore in lower intertidal species. Vermeij suggested that the former trend was the result of physical factors increasing the mortality of juveniles high on the shore. The large surface area to volume ratio of juveniles increases their susceptibility to desiccation (Lewis 1954; Davies 1969; Foster 1971). The latter trend was interpreted as being the result of adaptations by juveniles to settle high on the shore, in order to avoid the more intense biological interactions of lower areas. Bertness (1977) found the size of carnivorous gastropods to increase with decreasing tidal height; the size gradients of the gastropods were actively maintained. He concluded that this was a response to similar size gradients shown by prey species, promoting an energy efficient size selection relationship between predators and prey, and facilitating intra- and interspecific resource partitioning.

Intraspecific zonation is not restricted to gastropods, but also occurs among bivalves (Matthiessen 1960; Ansell and Lagarere 1980; Ansell 1983), crusteceans (Glynn *et al* 1975; Haley 1982) and polychaetes (Brown 1982). Changes in body size along tidal gradients are not always due to resource segregation, however. They can simply be a result of the increased feeding time available in lower areas of the beach (Lambert and Farley 1968). Alternatively, the distribution of individuals may be determined by physical processes. Matthiessen (1960) found that large bivalves tended to accumulate near changes in the beach slope, due to sorting by water currents. Sediment stability has also been shown to be an important factor controlling the distribution of organisms, particularly juveniles (Rhoads and Young 1970; Biernbaum 1979; James and Gibson 1980).

Spatial changes in the size distribution of suspension feeders may be related to adult-larval interactions. Woodin (1976) suggested that the filtering activities of suspension feeding adults may be a significant cause of larval mortality. There is some evidence to support this hypothesis (Williams 1980) but the role of adult ingestion of larvae in structuring benthic communities is not clear (Peterson 1982).

In the previous chapter, a hypothesis for the maintainance of the Pipe Clay Lagoon community structure was proposed. It was suggested that the vertical (along the tidal gradient) and horizontal (across the tidal gradient) segregation of organisms was largely

due to interactions among the fauna, mediated by physical characteristics of the beach. In the following section, evidence is sought for the existence of vertical interactions. The examination is based on the identification of serial correlations within and between species, and between species and physical parameters, along the distribution transects.

5.2 Methods

5.2.1 Introduction

A 'time series' is a collection of observations made sequentially in time. Time series analysis is concerned with identifying the non-random component(s) of the series. The choice of time as the dimension is not exclusive, however, and the methods developed for time series analysis may equally be applied to sequential measurements in another dimension, such as space. Thus, the series of species' abundance measurements made along a transect form series that are open to analysis by the methods of time series.

Kendall (1973) identified 5 objectives of (time) series analysis:

1. a concise description of the system's behaviour,

2. an explanation of the system's behaviour in terms of other variables and an underlying model,

3. use of (1) and (2) to forecast the behaviour of the system,

4. examination of the behaviour of the perturbed system by altering the model's parameters,

5. consideration of the joint progress of a number of variables.

In the case of transect series analysis, point (3) is not applicable because, in the present study, the transect covers the whole series, there being no extrapolation beyond the end of the intertidal zone (by definition).

A typical time series may be composed of 4 parts (Kendall and Stuart 1966):

1. a trend, or long term movement
2. oscillations about that trend
3. a seasonal effect
4. a random component.

Point (3) is not applicable to a transect series, unless there is some parameter(s) that fluctuates in a cyclic manner with distance down the transect. It is reasonable to assume that no cyclic processes are operating along the intertidal environmental gradient.

Series which exhibit long-term changes in mean are said to show 'trend' and are therefore 'non-stationary'. In a 'stationary' series the mean and variance are constant along the observational axis. In practice, series analysis only requires 'reduced stationarity' (Chatfield 1975), where the mean and variance depend only on the length of the segment considered and not on its position along the observational axis. However long a series may be, we can never be sure that what appears to be a trend is not really part of a slow oscillation; when the series has terminated (as in the intertidal transect) this problem does not arise.

In a stationary series, where the trend has been removed, the series will be represented by an oscillatory process. The objective of series analysis is to determine whether this residual series is systematic, with the oscillations able to be represented as some function of the observational axis. The alternative is for the oscillations to be random, in that they could have occurred in the observed order by random sampling from a homogeneous population. There may, of course, be some intermediate situation between the two extremes of complete functional variation and complete randomness.

There is a large variety of methods available for removing trend in a series before subjecting the resulting residual series to analysis. Often the trend itself is of interest, but, in all cases, trend removal is essential before the short-term (in relation to the observational axis) oscillations can be examined.

5.2.2 Trend fitting

Trend fitting inevitably requires a great deal of subjective judgement, meaning that it is important to fully set out the method by which the series has been filtered.

Kendall (1973) illustrated the subjectivity that is both an unavoidable and essential component of trend fitting. He showed that a trend fitting technique could be 'too good' if it followed the trend too closely. The objective is to filter out the trend in order to study the oscillations but a closely fitted curve can treat the oscillations about the trend as being part of that trend. Subtracting such a fitted trend from the primary series would remove most of the variation that is of interest. Ord (1979) suggested obtaining several trend plots and selecting the best of them by eye.

It is essential to the concept of trend that the long term movement of the series is smooth and can therefore be represented, at least locally, by a polynomial in the observational element (Kendall and Stuart 1966). In many cases, however, there will be no substantive meaning that can be given to the coefficients of the polynomial. If a polynomial is used to fit the trend, it is an advantage to use a polynomial of low degree since the curve will be smoother, the 'explanation' simpler and the function more economical; a disadvantage of using a polynomial of too low a degree is that it introduces a statistical bias in estimating the trend (Anderson 1971). At the other extreme, using a polynomial of too high a degree may be somewhat artificial. Also, the coefficients of such a polynomial, being based on high-order moments, would be unstable from the sampling viewpoint (Kendall and Stuart 1966).

Smoothing versus polynomial trend fitting

'Smoothing' involves representing the trend of a given series by a weighted average of the observed values near each point of the series. In this way, the irregular curve of

observations is filtered by a smooth curve. 'Smooth' is here taken in the sense that a smooth function can be adequately represented by a polynomial of fairly low degree over some reasonable span of time, or space (Anderson 1971). The polynomial that approximates the smooth function in one interval may be different to the approximating polynomial in other intervals. In practice, it is preferable to fit polynomials of the same order to each interval (Kendall 1973).

Fitting different polynomials to different parts of the series involves taking the first n terms (n arbitrary) and fitting a polynomial of degree less than or equal to $(n-1)$ to those terms. That polynomial is then used to determine the trend value in the middle of its range. The operation is repeated with the n terms from the second to the $(n+1)^{th}$ and so on, moving by one term each time. This procedure (Kendall and Stuart 1966) is a moving average technique.

The advantage of using smoothing to estimate trend is that it makes no rigid assumptions. However, because the method is not based on an explicit probability model, statistical inference is limited and it is not possible to test hypotheses about the trend, or to relate the trend to a model for the generation of the series (Anderson 1971). Smoothing results in a description, rather than an analysis or explanation, of the trend but this is sufficient for removing the trend prior to series analysis.

Smoothing by moving averages

The methodology for smoothing by the process of moving averages is discussed in detail by Kendall and Stuart (1966) and Kendall (1973). Only an outline of the major points will be provided here. The procedure uses the method of least squares to fit polynomials (of some chosen order) to different parts of the same series and then obtains a centered moving average.

Suppose, for the purposes of illustrating the notation, an average of sets of 4 terms of a series is taken, weighting each term equally. Then, if the primary series in dimension c is $\{u_d\}$ (the set of terms $u_1, u_2, \ldots, u_d, \ldots$) this will produce a new series $\{v_d\}$ where

$$v_1 = (u_1 + u_2 + u_3 + u_4)/4 \quad \text{etc.}$$

Taking a set-of-4 average of the new series will result in a series $\{w_d\}$ where

$$w_1 = (v_1 + v_2 + v_3 + v_4)/4$$

$$= (u_1 + 2u_2 + 3u_3 + 4u_4 + 3u_5 + 2u_6 + u_7)/16 \quad \text{etc.}$$

Symbolically, the weights of the coefficients can be written as

$$\{[1,1,1,1]/4\}^2 = [1,2,3,4]/16$$

where 4 represents the point of symmetry,

i.e. $[1,2,3,4]/16 = [1,2,3,4,3,2,1]/16$.

In practice, it is more convenient to take averages over an odd number of terms to facilitate centering the average. Let

$2m + 1$ = the (odd) number of terms over which the averaging will take place (m an integer)

p= the degree of the polynomial(s) used to fit the trend.

Since the average is over $2m + 1$ terms, those terms will be centred about a term, say u_0, of the series in the following manner:

$$u_{-m}, u_{-(m-1)}, \ldots, u_0, \ldots, u_{m-1}, u_m .$$

Suppose the central term, u_0, assumes a value a_0 at $d = 0$, where the series is described in terms of the observational dimension, d. Kendall and Stuart (1966) showed that

$$a_0 = c_0 + c_1 u_{-m} + c_2 u_{-(m-1)} + \ldots + c_{2m+1} u_m$$

where the constants $\{c\}$ are independent of $\{u\}$ but dependent on m and p.

The process of fitting a trend line consists of determining the constants $\{c\}$ and then calculating, for each consecutive set of $(2m + 1)$ terms in the series, a value for the centered average, a_0. If the terms are $u_x, \ldots, u_{2m+x}$ this calculated value will correspond to $d = m + x$.

A supplementary procedure is required to give values corresponding to the first and last m terms.

In general, the case p odd includes the case for the next lowest (even) value of p. Thus, the formulas for the weights of the moving averages for the quadratics and cubics are the same, as are the formulas for quartics and quintics.

Kendall and Stuart (1966) give the formulas for quadratics/cubics for $2m + 1 = 5$ to 21 and for quartics/quintics for $2m + 1 = 7$ to 21. For a given m and p, the trend values T_d at point d on the series are calculated by applying the appropriate formula to the terms

$$u_{d-m}, \ldots, u_d, \ldots, u_{d+m}$$

of the series (obviously $d > m$). This can be illustrated by using Kendall and Stuart's example (1966, p.368). The moving average formula for $m = 3$ and $p = 3$ is given by

$[-2,3,6,7]/21$.

If the $2m + 1 = 7$ terms of the series to be averaged are

$u_{d-3} = 0$, $u_{d-2} = 1$, $u_{d-1} = 8$, $u_d = 27$, $u_{d+1} = 64$, $u_{d+2} = 125$, $u_{d+3} = 216$,

then the average, centred on d is given by

$$T_d (= a_0) = \{(-2 \times 0)+(3 \times 1)+(6 \times 8)+(7 \times 27)+(6 \times 64)+ (3 \times 125)+(-2 \times 216)\}/21$$
$$= 27.$$

End effects

It is obvious that the moving average technique fails to provide trend values for the first and last m terms of the series. The gaps can be filled by calculating a_j (rather than a_0) for the terms

$$u_{-m}, u_{-(m-1)}, \ldots, u_{-1}$$

at the first end of the series and for

$$u_{+1}, \ldots, u_{m-1}, u_m$$

at the last end, where the terms over which the average is centred are, as before,

$$u_{-m}, \ldots, u_0, \ldots, u_m.$$

The formulas for the coefficients have been calculated by Cowden (1962, cited by Kendall 1973) and are listed by Kendall (1973) as an appendix. As an example, again with $m = 3$ and $p = 3$, the formulas for the first 3 terms in this 7-point moving average are

[39,8,-4,-4,1,4,-2]/42 , [8,19,16,6,-4,-7,4]/42

and [-4,16,19,12,2,-4,1]/42 respectively.

Note that the weighting coefficient vectors are no longer internally symmetrical.

By symmetry, the formulas for the last 3 terms are

[1,-4,2,12,19,16,-4]/42 , [4,-7,-4,6,16,19,8]/42

and [-2,4,1,-4,-4,8,39]/42 respectively.

Thus, if the last 7 terms of a series are

0,1,8,27,64,125,216 ,

the last term of the fitted trend will be

$$T_{last} = [(-2 \times 0)+(4 \times 1)+(1 \times 8)+(-4 \times 27)+(-4 \times 64)+ (8 \times 125)+(39 \times 216)]/42$$
$$= 216$$

(which exactly corresponds with the observed term since, in this case, a cubic is being fitted with a cubic).

5.2.3 Analysing the variability of a stationary series

Having removed the trend from the observed series, the residual series will be stationary and can then be subjected to analysis by extensions to basic statistical methods, including autocovariance and autocorrelation. These methods measure the relationship between successive terms of the series.

Autocorrelation (serial correlation)

Sample autocorrelation coefficients measure the correlation between observations at different distances apart (i.e. different 'lags').

Given n values of a series $u_1, u_2, \ldots, u_n$, the autocorrelation at lag k is the corrrelation between pairs of terms k units apart, given by

$$r_k = \frac{(n-k)^{-1}\left[\Sigma\left[\left(u_i - (n-k)^{-1}\Sigma u_i\right)\left(u_{i+k} - (n-k)^{-1}\Sigma u_{i+k}\right)\right]\right]}{\sqrt{\left[(n-1)^{-1}\left[\Sigma\left(u_i - (n-k)^{-1}\Sigma u_i\right)^2\right](n-k)^{-1}\left[\Sigma\left(u_{i+k} - (n-k)^{-1}\Sigma u_{i+k}\right)^2\right]\right]}}$$

(Kendall and Stuart 1966; a typographical error was corrected in Kendall 1973). Here all summations, $\Sigma = {}_{i=1}\Sigma^{n-k}$.

This formula measures the first $(n-k)$ u's about their mean. For simplicity, the measurements may be made about the mean of the whole set of observations and also the variance for the whole series. The formula for r_k then reduces to

$$r_k = \frac{(n-k)^{-1}\left[{}_{i=1}\Sigma^{n-k}\left(u_i - \hat{u}\right)\left(u_{i+k} - \hat{u}\right)\right]}{n^{-1}\,{}_{i=1}\Sigma^{n}\left(u_i - \hat{u}\right)^2}$$

where $\hat{u}$ is the mean of $\{u_i\}$.

This is the form for common use (e.g. the IMSL statistical package). Kendall and Stuart (1966) note, however, that this approximation is not suitable for 'short' series, and may result in $|r_k| > 1$. Although no figure was placed on 'short' by those workers, generally 100 or more observations is considered 'large' enough for series analysis (e.g. Legendre and Legendre 1983). The transects conducted in the present study contain 36 observation points. For this reason, the exact formula for r_k was used, in preference to its approximation.

5.2.4 Cross-correlation between two stationary series

The approach to analysing the variability within a single stationary series can be extended to analyse variability between two stationary series. Legendre and Legendre (1983) describe a method for calculating the cross-covariance between two series, using the means of the two truncated series.

For two series, $\{u_{ih}\}$, $\{u_{jh}\}$ calculate

$$\hat{u}_i = (n-k)^{-1} \sum_{h=1}^{n-k} u_{i(h+k)}$$

and

$$\hat{u}_j = (n-k)^{-1} \sum_{h=1}^{n-k} u_{jh}$$

where n and k are defined as before but with the important proviso that the series $\{u_{ih}\}$ leads the series $\{u_{jh}\}$ by k units.

The cross-covariance between $\{u_{ih}\}$ and $\{u_{jh}\}$ at lag k is then

$$c_{ij}(k) = (n-k-1)^{-1} \sum_{h=1}^{n-k} (u_{i(h+k)} - \hat{u}_i)(u_{jh} - \hat{u}_j).$$

Note that $c_{ij}(k) = c_{ji}(k)$.

If $k = 0$, $c_{ij}(0)$ is the covariance between the two series. The cross-correlation between the two series at lag k is then

$$r_{ij}(k) = \frac{\Sigma(u_{i(h+k)} - \hat{u}_i)(u_{jh} - \hat{u}_j)}{\sqrt{[\Sigma(u_{i(h+k)} - \hat{u}_i)^2 \Sigma(u_{jh} - \hat{u}_j)^2]}}$$

where $\Sigma = \sum_{h=1}^{n-k}$, as before.

This formula is not equivalent to the exact extension to that of the autocorrelation formula but, in the present study, no spurious correlation coefficients were encountered during its use.

5.2.5 Correlograms (the sample correlation functions)

If values of r, either as r_k or $r_{ij}(k)$, are obtained for $k = 0, 1, 2, \ldots$ (note that $r_0 = 1$ and $r_{ij}(0) = 1$), then a correlogram plotting r as ordinate and k as the abscissa

can be constructed. Cox and Lewis (1966) noted that $r\sqrt{(n-1-k)}$ is normally distributed for large n. Approximate tests of significance for r can therefore be formed, with the null hypothesis, $r = 0$, being rejected if

$|r| \geq 1.645/\sqrt{(n-1-k)}$ (10% level of significance)

$|r| \geq 1.960/\sqrt{(n-1-k)}$ (5% level of significance)

$|r| \geq 2.576/\sqrt{(n-1-k)}$ (1% level of significance).

Chatfield (1975) cautions that care must be taken in interpreting correlograms. At the 5% level of significance, for example, given that the data really are random (i.e. $r = 0$ for $k > 0$), 1 out of 20 values of r would be expected to appear 'significant' by chance. As a general rule, Chatfield suggests that there is little point in calculating r for values of k greater than about $n/4$. For the transect series, this translates to about $k = 9$, corresponding to a distance of 180 m, and neglecting values of k above 9 does not appear unreasonable. With $k \approx 20/2$, no values of r would be expected to appear significant by chance alone (at the 5% level).

5.2.6 Analysis of Pipe Clay Lagoon data

The series analysis, both auto- and cross-correlation, was conducted by the FORTRAN computer program CEREAL/CROSS, developed and written for that purpose (described in Appendix A).

The distribution transects provided an observed series for each size class of each species. These series were subjected to autocorrelation analysis for lags of $k = 0$ to 9. The large overall number (approximately 170) of size classes in the transect data makes it impractical to subject the mollusc assemblage to such a thorough cross-correlation analysis. Clearly, there is an overwhelming number of permutations (not combinations since the order by which one series leads the other is important) of species' size classes, taken in pairs for cross-correlation analysis.

To enable cross-correlation analysis, the size classes were pooled according to the scheme in Table 5.1. These groups do not always correspond to those used for the demographic analysis in Chapter 4, and represent a subjective compromise between a desire for detail and the need for practicality.

Autocorrelation analysis was conducted with the species groupings. The principal advantage of the groupings, however, is that they reduced approximately 170 size classes to 30 groups, allowing cross-correlation analysis. This was conducted for all permutations of species group pairings, for lags $k = 0$ to 5 and also $k = 10$. The limitation on the number of lags, compared to those of the autocorrelation analysis, was essential to prevent the results of the analysis becoming more unwieldy than the original data.

Table 5.1 :Species size class groupings and abbreviations.

Species	Group	Size Classes	Abbreviation
Anapella	I	0 mm	AcI
	II	1 mm	AcII
	III	2 mm	AcIII
	IV	3 - 6 mm	AcIV
	V	7 - 23+ mm	AcV
	Total	All	AcT
Hydrococcus	I	0 mm	HbI
	II	1 mm	HbII
	III	2 mm	HbIII
	IV	3 - 4+ mm	HbIV
	Total	All	HbT
Zeacumantus	I	0 - 1 mm	ZdI
	II	2 - 4 mm	ZdII
	III	5 - 12+ mm	ZdIII
	Total	All	ZdT
Katelysia	I	0 mm	KsI
	II	1 mm	KsII
	III	2 - 6 mm	KsIII
	IV	7 - 17 mm	KsIV
	V	18 - 30+ mm	KsT
Salinator	I	0 - 1 mm	SfI
	II	2 - 10+ mm	SfII
	Total	All	SfT

As discussed previously, there is a great deal of subjective judgement in selecting the best filter to remove the trend from a series prior to series analysis. With the autocorrelation analysis, it was feasible to construct correlograms for all possible orders of polynomial and ranges of moving averages allowed by CEREAL/CROSS. The polynomial power and moving average range combinations are:

power	range
2	5,7,9,11
3	5,7,9,11
4	7,9,11
5	7,9,11

With the cross-correlation analysis, however, the trend fitting was restricted to polynomials of power 3.

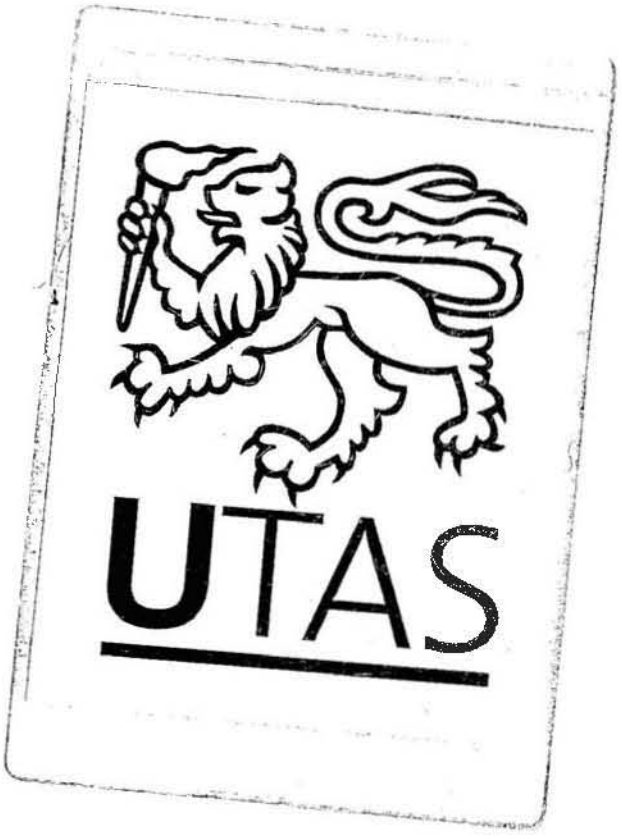
Ord (1979) suggests selecting the best fit of the trend by eye. Here it was decided to make the selection after the analysis, by examining the correlograms. The correlograms were calculated for each possible moving average range (5,7,9,11) for lags k =0 to 5 and k = 10. These correlograms were examined and the 'best' power/range combination was selected, as described in Section 5.3.

Only the correlograms for the selected filter are presented here. In the strict sense, they are not actually presented as true, graphical correlograms. Since the cross-correlograms from the selected filter alone comprise approximately 25,000 correlation coefficients, it was decided to present only the significant (at the 10, 5 and 1% levels) coefficients. Even then, the actual coefficients are not listed, only their significance.

In addition to the within and between species group(s) series correlation analysis, each species group was analysed for cross-correlation with the physical parameters described in Chapter 2. All these analyses were conducted for lag $k = 0$ only, with no prior filtering of either series. This was a deliberate choice since the biological significance of correlations between organisms and physical parameters some distance away on the tidal-flat was considered to be doubtful.

It could be argued that the physical and/or species series should have been filtered in these analyses. However, it was decided that the filtering of a physical parameter, say beach height, was nonsensical. For beach height, for example, the primary influence of that parameter is its trend and removing that trend would remove any possibility of examining its role. Having defined all other 'physical parameters' as being physical (including worm tubes and algal mats), they were treated similarly. The species series

were also left unfiltered in that analysis in order to allow the detection of trend attributable to the trend of the physical parameters.



5.3 Results

5.3.1 Introduction

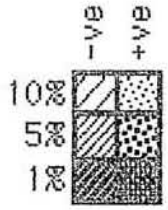
In this, and subsequent chapters, a standard form of results presentation is used. The results, which effectively represent reductions of the original data sets, are themselves complicated and a standard form of presentation is considered necessary.

The reductions can perhaps be best appreciated if the body of correlation coefficients or test statistics is thought of as being sliced through at different levels of significance. Only those terms above the cutoff are considered further but the act itself is only a means to an end and not a formal test. Thus, the results of the analyses need to be further inspected. No rigid statistical analyses are possible *a priori* since it is only by inspection of the results that hypotheses can be generated. The analyses presented in Chapter 5 (and 6) are therefore exploratory analyses of the data and are not formal tests of hypotheses.

By choosing a number of levels of significance, the data sets can be examined with different levels of fidelity; 10, 5 and 1% were selected to provide a geometric increase. A further factor that must be considered with correlation coefficients and test statistics is the sign of those terms. In total, this gives 6 levels of inspection. These levels are identified throughout this work by the shading patterns presented in Table 5.2.

It is important to recognise that the size 'groups' considered here are amalgamations of the size 'classes' of former chapters.

Table 5.2 : Identification patterns for the sign (+ve or -ve) and level of significance (10, 5 or 1%) of correlation coefficients and test statistics.



5.3.2 Serial correlation with physical parameters (Fig. 5.1)

The serial correlations of the species' groups with the defined physical parameters in each season are shown in Fig. 5.1.

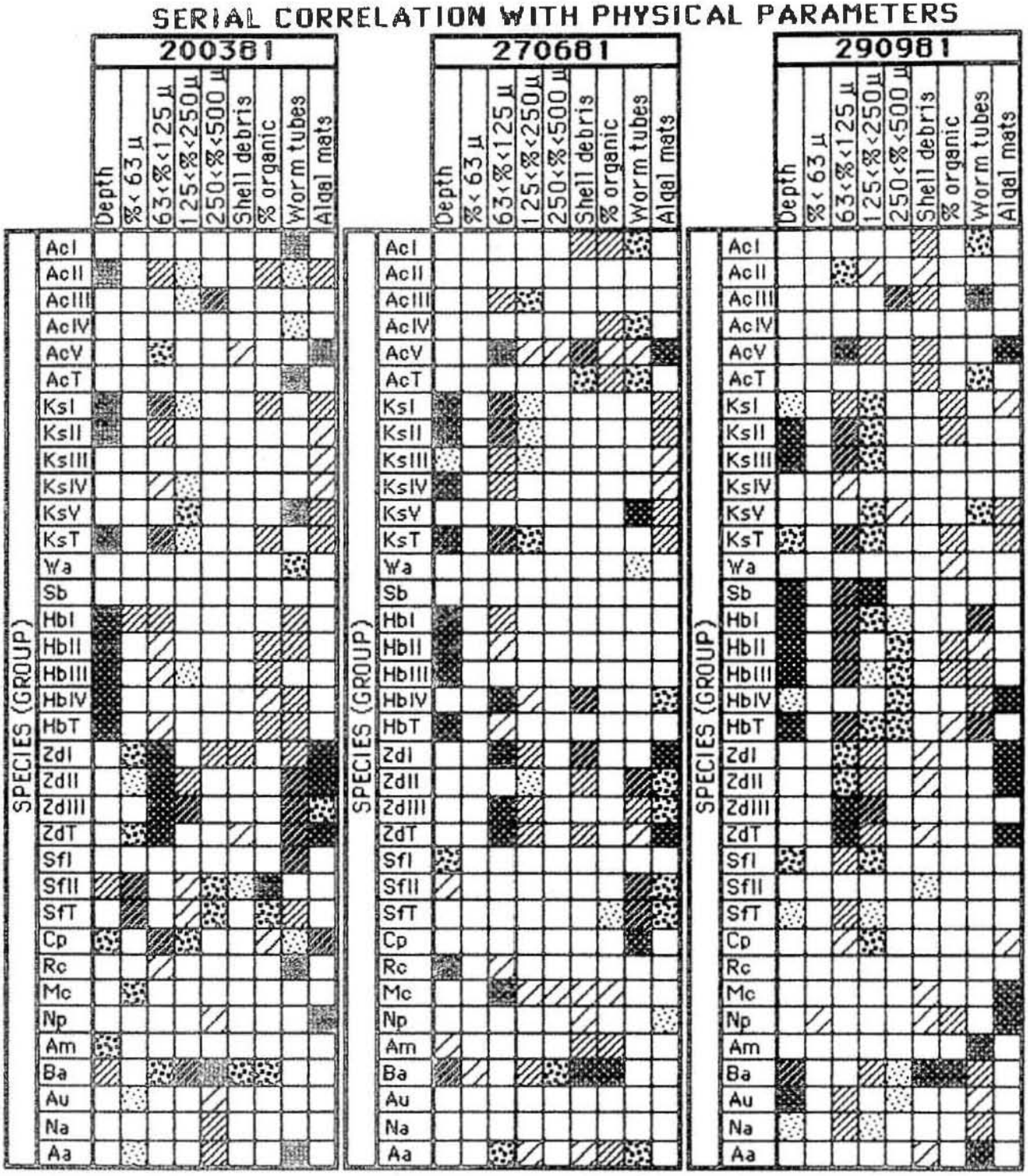


Fig. 5.1 Serial correlation analysis (lag=0) of species groupings with physical parameters. Species abbreviations as in Table 5.1. Shadings indicate sign of correlation and level of significance as defined in Table 5.2.

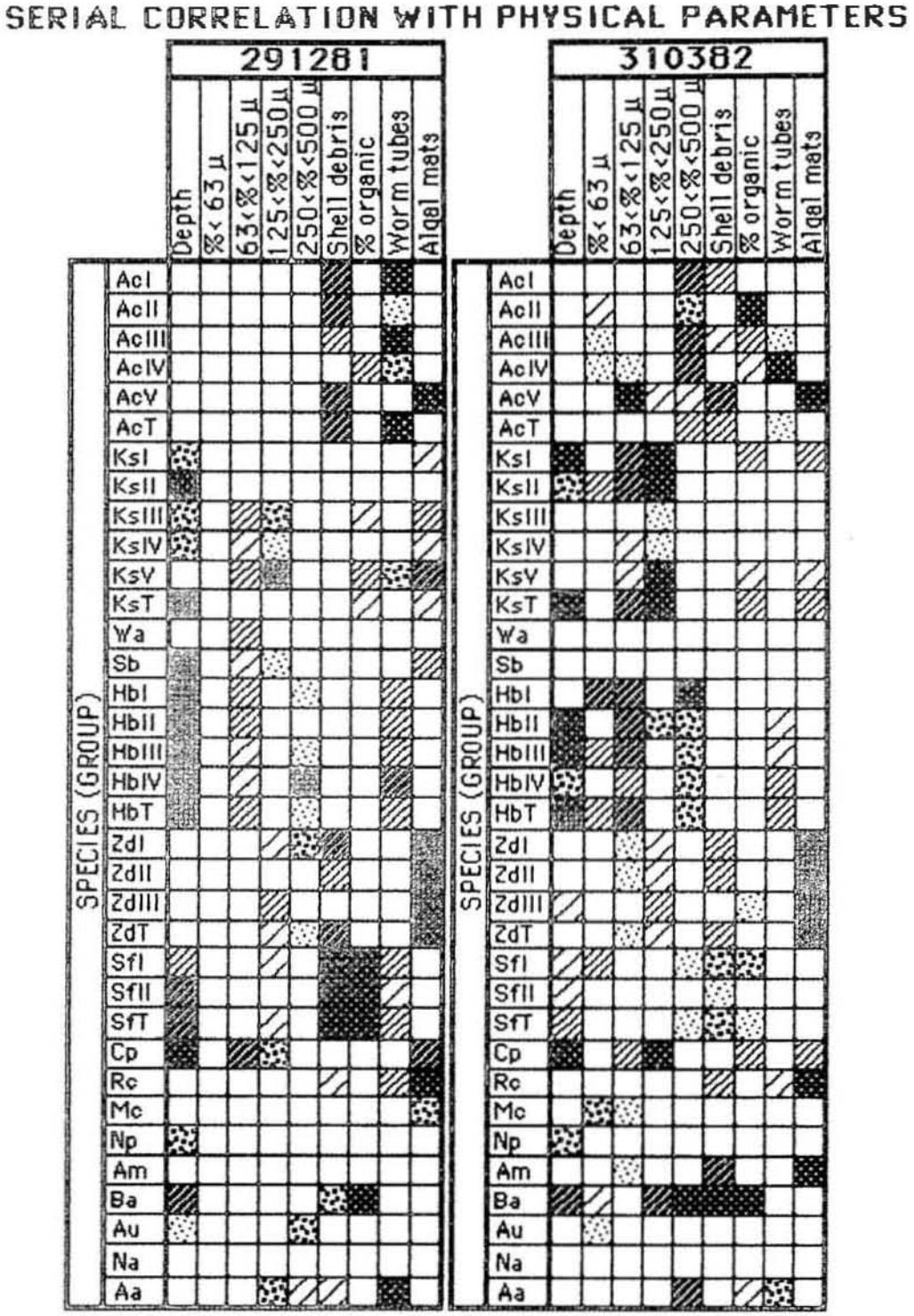


Fig. 5.1 (continued)

Beach depth

Only 4 species show consistent correlations between abundance and beach depth: *Katelysia* , *Hydrococcus* , *Salinator* and *Bembicium* .

Katelysia is positively correlated with depth in all seasons. In both autumn samples this is restricted to the first two groups (and total) while in the other seasons the correlations extend to the larger size groups. Correlations are strong throughout.

Hydrococcus also exhibits strong positive correlation with depth in all seasons. This is true for all size groups except group IV in winter and spring and group I in the 310382 autumn.

The sign of the correlations of *Salinator* varies with the group and season. Group I correlation is negative in summer and autumn but positive in winter and spring. Group II correlations are negative, except in spring when they are negligible, while the *Salinator* total correlations generally appear to reflect those of group I.

The correlations of *Bembicium* are always strongly negative.

Sediment fractions

Correlations between animal distributions and sediment < 63 μ are only significant in the autumn seasons. In the 200381 autumn, these are restricted to the gastropods. *Hydrococcus* (group I) and *Salinator* (except group I) correlations are negative while *Zeacumantus* (except group III) and *Microdiscula* have positive correlations. On 310382 *Anapella* and *Katelysia* group II animals have negative correlations but *Anapella* group III is weakly positive. *Hydrococcus* and *Salinator* correlations are again negative but different groups are involved (HbI, HbIII, SfI). *Microdiscula* has the same level of correlation in both autumns. No significant correlations exist for *Zeacumantus* .

Correlations between the distributions and the sediment fraction between 63 μ and 125 μ are strong in most seasons, the weakest season overall being summer. A number of species/groups exhibit consistent relationships with the sediment fraction - *Katelysia* , *Hydrococcus* and *Zeacumantus* in particular. Most *Katelysia* and *Hydrococcus* groups have strong, negative correlations in all seasons (HbIV is strongly positive in winter) while *Zeacumantus* is typically strongly positive (weak on 310382).

Of the other species, *Anapella* group V animals have strong positive correlations in all seasons but summer; in winter this probably accounts for the similar correlation of the epizoic *Anthopleura* . *Cylichnina* is negatively correlated in autumn and summer, *Microdiscula* is positive in autumn and summer and *Bembicium* is positive in

autumn.

In general, the correlations with the larger sediment fractions (125-250 μ and 250-500 μ) are opposite in sign to the above. Overall, correlations are relatively weak with the largest size fraction and, in fact, are negligible for *Katelysia* and *Zeacumantus*.

Shell debris

Correlations between the distributions and shell debris are relatively weak in the 200381 autumn, the winter and the spring. In those seasons they loosely reflect the correlations of the larger sediment size fractions although *Katelysia* and *Hydrococcus* appear largely unrelated to shell debris while negative correlations for *Anapella* are introduced.

Correlations are particularly high in summer, most noticeably with most groups of *Anapella* and *Zeacumantus* (negative) and also *Salinator* (positive). These correlations persist through to the 310382 autumn although their significance decreases.

Organic content

The principal features of the correlations between species distributions and organic content of the sediment are the generally moderate negative correlations shown by *Anapella* (and to a lesser extent, *Katelysia*) and the strong positive correlations shown by *Salinator*. A deviation from this pattern is the high positive relationship of group II *Anapella* in the 310382 autumn. The negative correlations shown by *Anthopleura* probably reflect those of *Anapella*.

Bembicium shows consistently high positive correlations while *Hydrococcus* is negatively correlated in the 200381 autumn and the spring.

Worm tubes

There is considerable seasonal variation in the correlation patterns between the species distributions and the distribution of the polychaete worm tubes.

Most groups of *Anapella* have moderate to high positive correlations in all seasons but *Katelysia* correlations are negligible except for group V which is typically high and positive. *Hydrococcus* correlations are generally negative but are negligible in winter. Strong negative correlations exist for *Zeacumantus* on 200381 and 270681 but are negligible in other seasons. *Salinator* is also negative in seasons other than spring and the 310382 autumn. A strong positive correlation for *Cylichnina* exists in winter. The common positive relationships shown by *Anthopleura* are probably associated with those of *Anapella* and *Katelysia*.

Algal mats

Anapella group V has a strong positive correlation with the algal mats in all seasons but the correlations of other *Anapella* groups are negligible. In contrast, most groups of *Katelysia* are negatively correlated (only I and V on 290981 and 310382). *Zeacumantus* groups are typically strongly positive in all seasons, while *Cylichnina* is generally negative. *Rissopsis* has strong positive correlation on 291281 and 310382.

5.3.3 Autocorrelation series analysis of distributions

The autocorrelation correlograms are presented in Appendix B. As described in Section 5.2.6, all possible combinations of polynomial powers and moving average ranges (out of the defined selection) were used for the autocorrelation analyses. This allows an examination of the role of those chosen parameters in determining the apparent within-species relationships.

Relatively few species exhibit significant serial autocorrelation; summer is the principal season for autocorrelation. *Katelysia* shows autocorrelation within a number of its groups in all seasons. Autocorrelation is significant within *Hydrococcus* groups in autumn (both samples) and winter but not in other seasons. Autocorrelations are significant for *Cylichnina* in the 200381 autumn and the summer, *Rissopsis* in winter, *Nassarius* and *Austrocochlea* in spring and summer and *Wallucina* and *Soletellina* in summer. No other species have significant autocorrelations in any season.

In general, most significant autocorrelations occur in distributions filtered using polynomials of power 2 (most ranges) or power 3 (ranges 9 and 11). Also, a number of patterns common to different groups in different seasons are evident.

Katelysia

In the 200381 autumn *Katelysia* 1 mm animals are negatively autocorrelated at lag 1 (a lag of 20 m) while being positively autocorrelated at lags 4 and 6. Either side of the latter lags the correlations are positive, suggesting a cyclic pattern of negative and positive autocorrelations at a 20 m scale. The relatively high representation of 1 mm animals in the overall species total probably account for the approximately similar autocorrelations shown by the total.

In winter the 11 mm and 19 mm size classes show significant autocorrelations. For the 11 mm class these are negative at lag 1, positive between lags 2 and 4 and negative at lags 5 and 6. The 19 mm class also exhibits strong negative correlation at lag 1 but lags 2 and 3 are generally negative while lags 4 and 5 have positive values.

Several *Katelysia* size classes and one size group have significant correlations in spring; these are characterised by being comparatively widely scattered over the possible lags. Although all significant correlations at lag 1 are negative, only the 7 mm class has an extension of the negative correlations to lags 2 and 3; for this class the pattern is very similar to that of the 19 mm animals the previous winter. The other classes, which make up group III, typically have negative values at lag 1, positive at lag 4 and negative at lag 6. The 3 mm class then shows an alternation of sign to lag 9.

Numerous *Katelysia* size classes exhibit significant autocorrelations in summer. A number of these classes (2, 9 and 14 mm) have patterns in common, patterns very similar to those of the 11 mm animals in winter. The 10 mm class pattern is similar to that of the 19 mm class in winter. The other classes (and the total) have comparatively few significant terms; the 4 mm class values are strongest and their signs approximately alternate between positive and negative between lags 5 and 9.

Correlations are generally weak within *Katelysia* classes in the 310382 autumn; the 1 mm class is negative at lag 1 under most filters.

Wallucina and *Soletellina*

Both these species have strong autocorrelations only in summer. The 5 mm *Wallucina* and *Soletellina* size class patterns are virtually identical to the 10 mm *Katelysia* pattern in that month while the 6 mm *Soletellina* pattern is very similar to the 2, 9 and 14 mm *Katelysia* patterns.

Hydrococcus

In the 200381 autumn only the 0 mm class has marked autocorrelation. This appears to be generally negative at lags less than 3 and positive at greater lags.

The same size class has an alternation of sign, from negative at lag 1 through to positive at lag 4, in the winter

In the 310382 autumn the correlations (in this season it is the 2 mm and 3 mm classes) are typically negative at lag 1 with little significance at other lags.

Cylichnina

Cylichnina has significant autocorrelations on 200381 and 291281 but these are strong only on the former date. In that season the pattern is very similar to that of the 19 mm *Katelysia* class in the winter.

Rissopsis

In winter *Rissopsis* has minimal significance of autocorrelation, being negative at lag 2.

Nassarius

In spring the 12 mm *Nassarius* class has a significance pattern similar to that of the 19 mm *Katelysia* animals in winter. In summer the general pattern (in small classes) is close to that of the winter 11 mm *Katelysia* class.

Austrocochlea

The 19 mm *Katelysia* winter pattern is also repeated in *Austrocochlea* in spring. The summer *Austrocochlea* pattern is different, with positive autocorrelation at lags 4, 8 and 9 and negative values at intermediate lags.

Two patterns occur repeatedly, and are characterised by those of the 11 mm and 19 mm classes of *Katelysia* in winter. Otherwise, there is a general tendency for small lags to be associated with negative autocorrelations with succeeding lags alternating in sign. Significant values are most common in quadratic and cubic filters and tend to occur most frequently in the filters having larger ranges of moving averages.

5.3.4 Cross-correlation series analysis of distributions (Fig. 5.2)

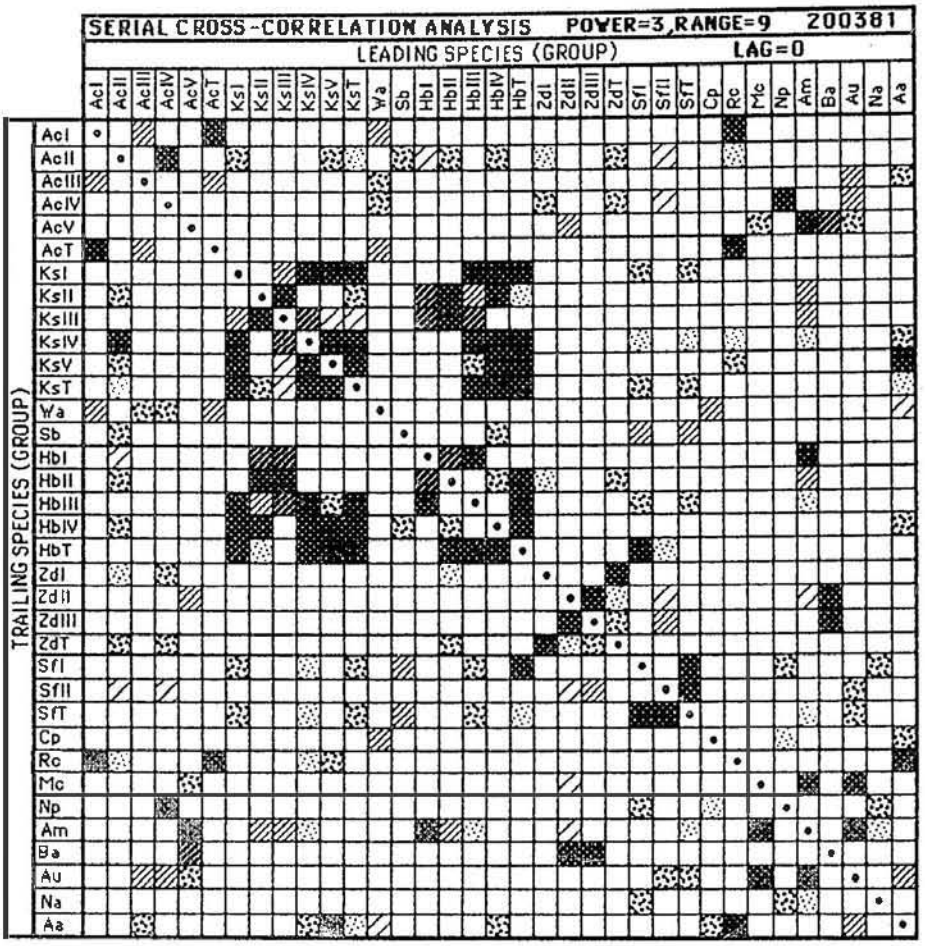
5.3.4.1 Introduction

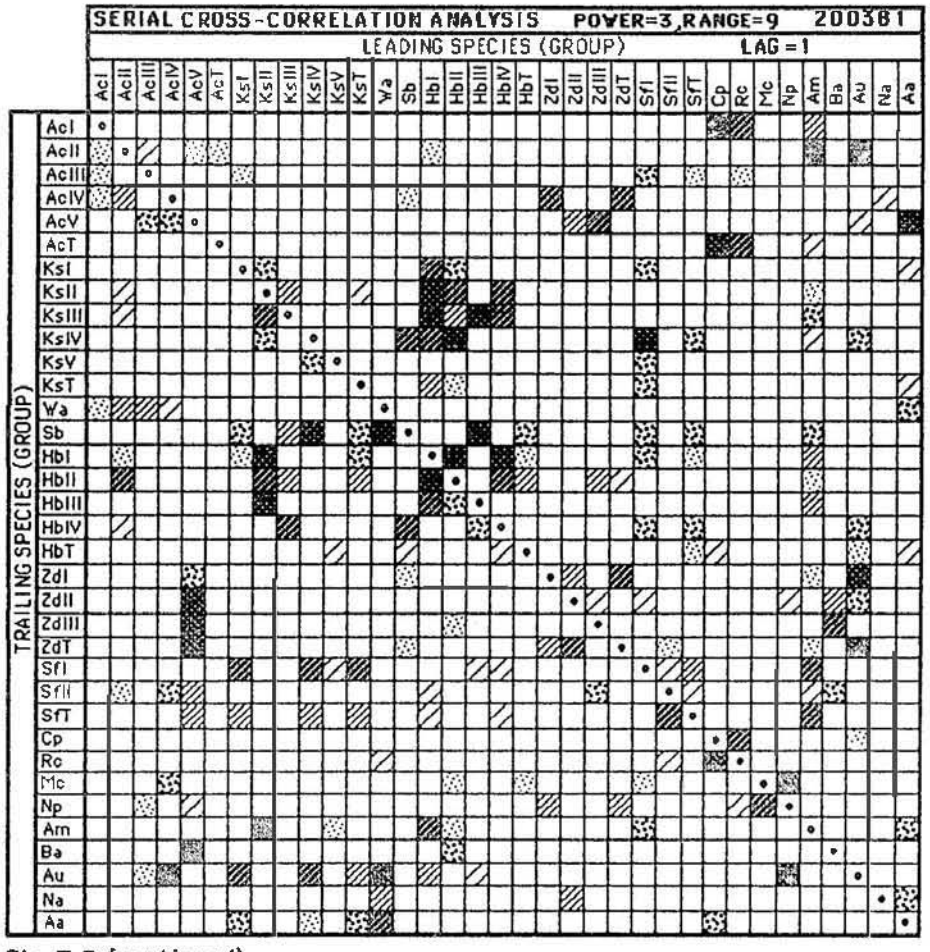
Although cubic filters using all (5, 7, 9, 11) moving average ranges were applied to the data, only the results from the range 9 filter are presented here. This filter was selected as being the most suitable and represents a compromise between trying to use as small a range as possible (to remove as much trend as possible) while not confusing the residual fluctuations with trend.

The smaller range filters were characterised by similarly patterned correlograms at all lags with an alternation of sign between successive lags. This probably results from the 'trend' following the actual series too closely, removing all but the random elements from the series. The random fluctuations would tend to lie above and below the trend in equal proportions and therefore two successive lags would be likely to pick up fluctuations of opposite sign, producing the alternating correlograms. This was most noticable with the smallest (5) range but decreased with increasing range and is not apparent with the range 9 filter. The significant cross-correlations between the filtered species/group distributions at the various lags are shown in Fig 5.2. These are presented for each season, including both autumn samples.

The interpretation of Fig. 5.2 is based on a recognition of the relationship between the leading and trailing species in the analysis. By definition, the series (distributions) run down the beach and forcing one species to lead another is equivalent to mathematically shifting the trailing distribution down the beach. Correlations are therefore made between the values of the leading series at given points on the beach and the values of the

Fig. 5.2 Serial cross-correlation analysis of species groupings filtered with a polynomial of power 3 over a moving average range of 9 (180 m). Correlations are calculated for lags 0 to 5 (0 m to 100 m). Species abbreviations as defined in Table 5.1. Shadings indicate sign of correlation and level of significance as defined in Table 5.2.





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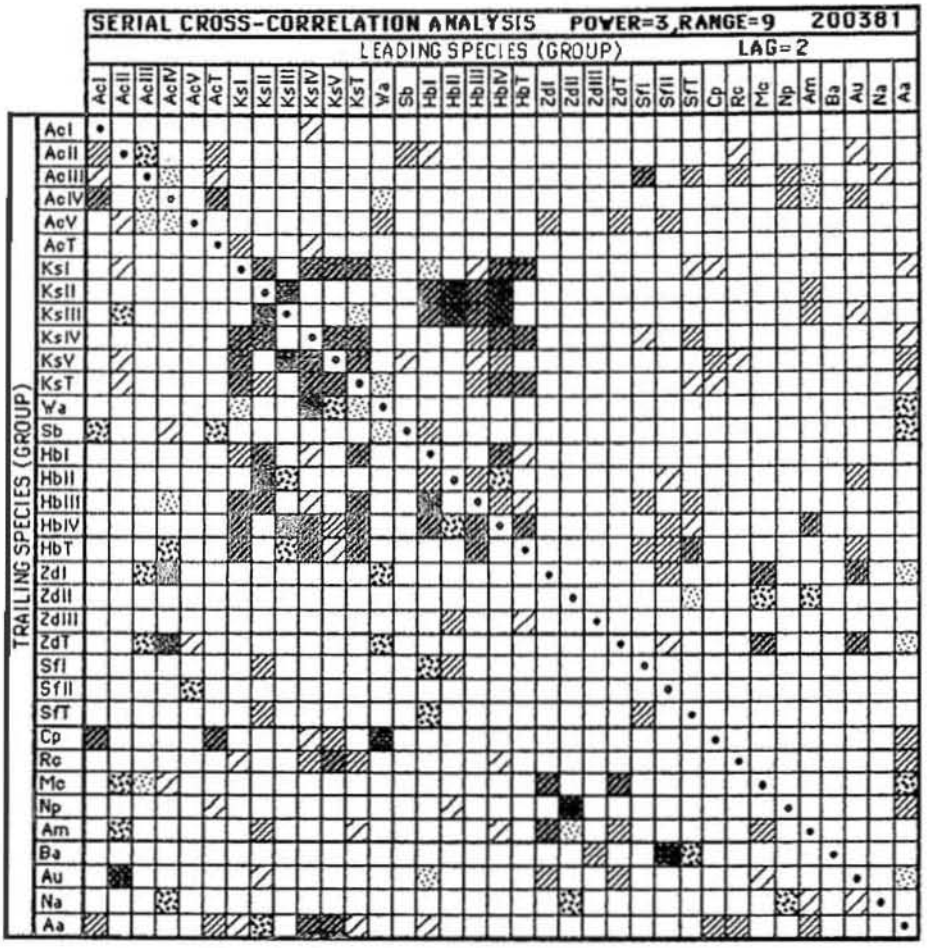

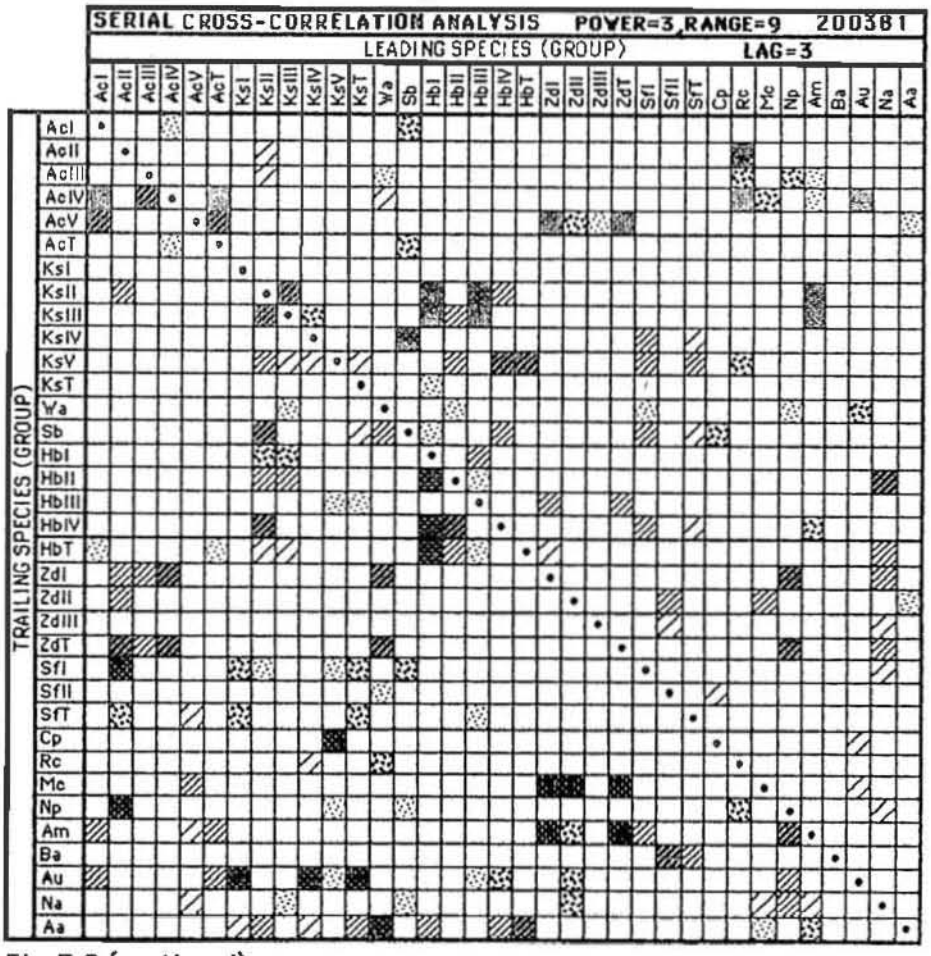

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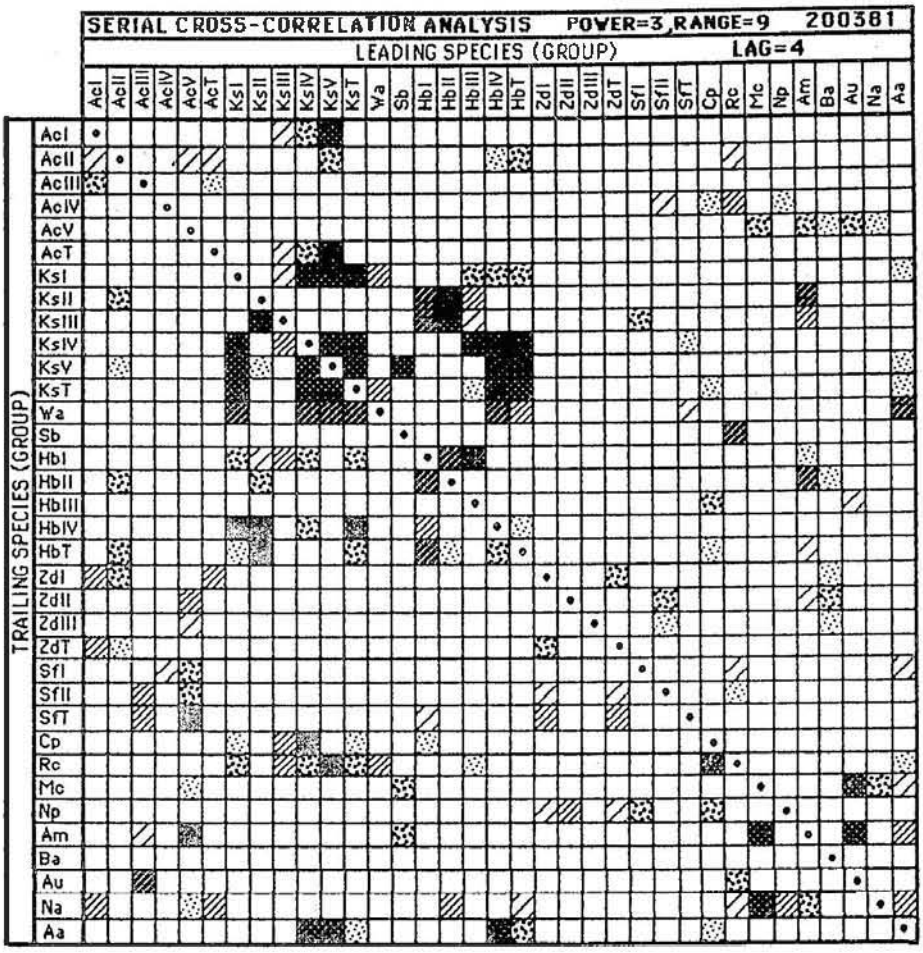

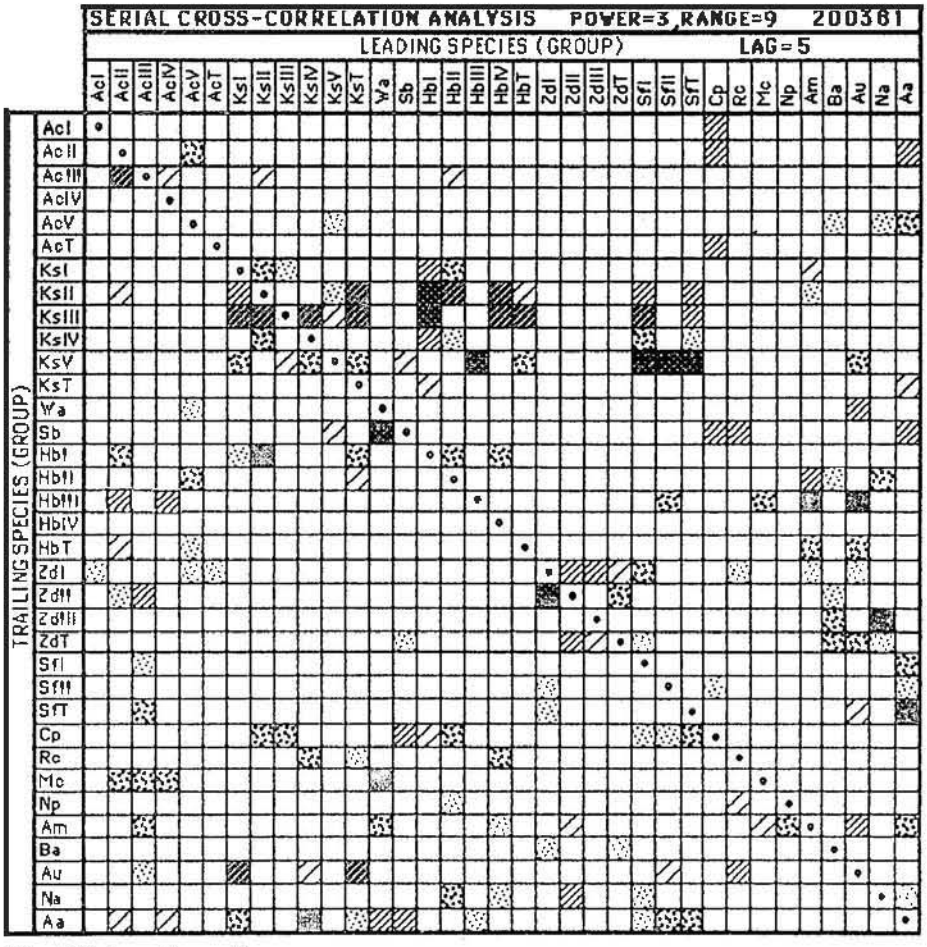

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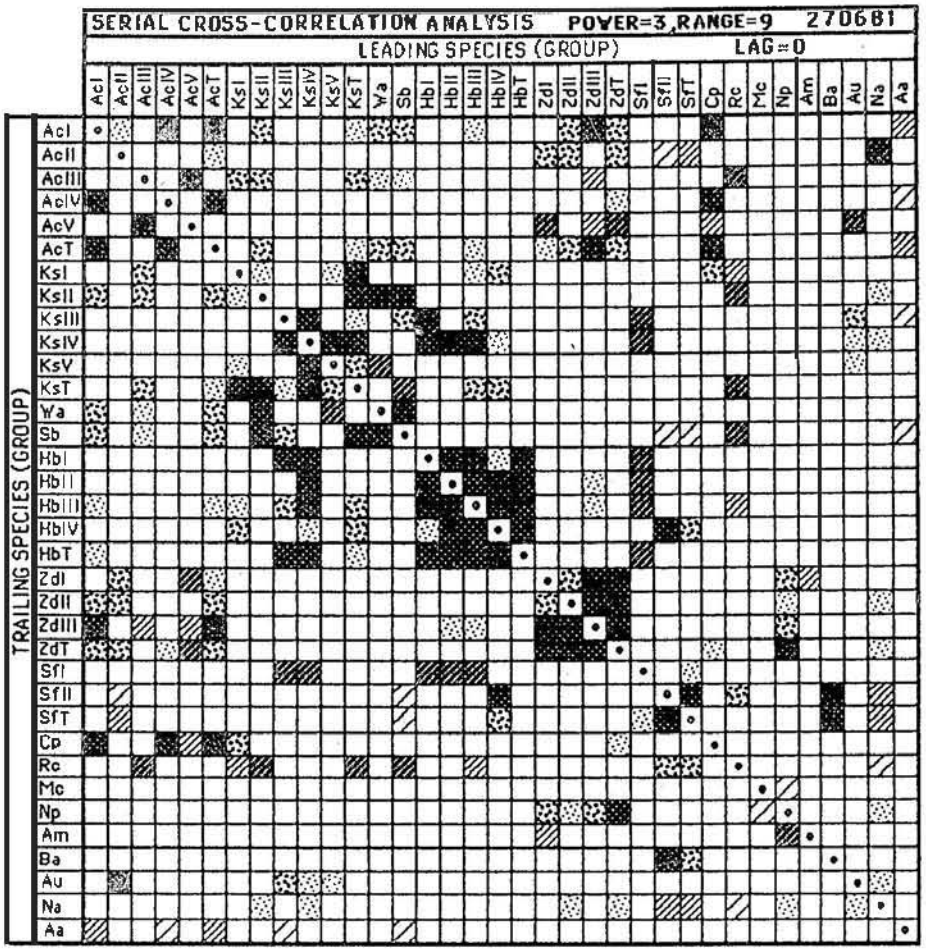

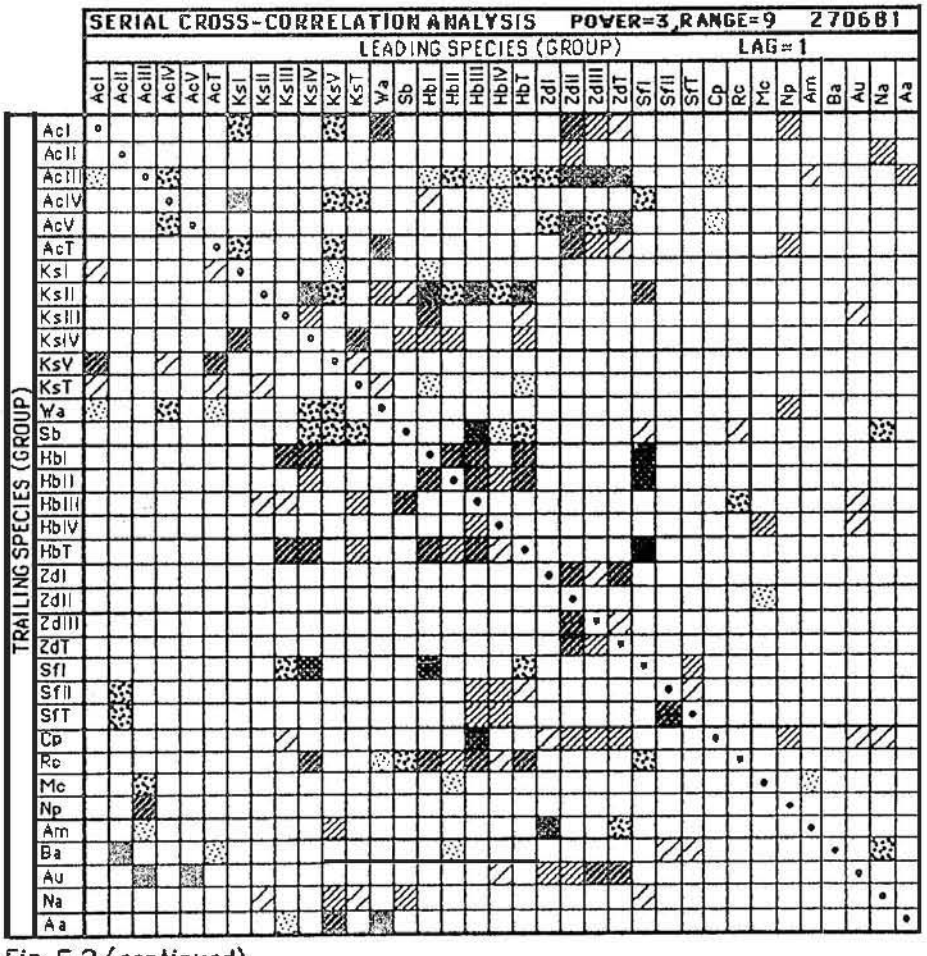

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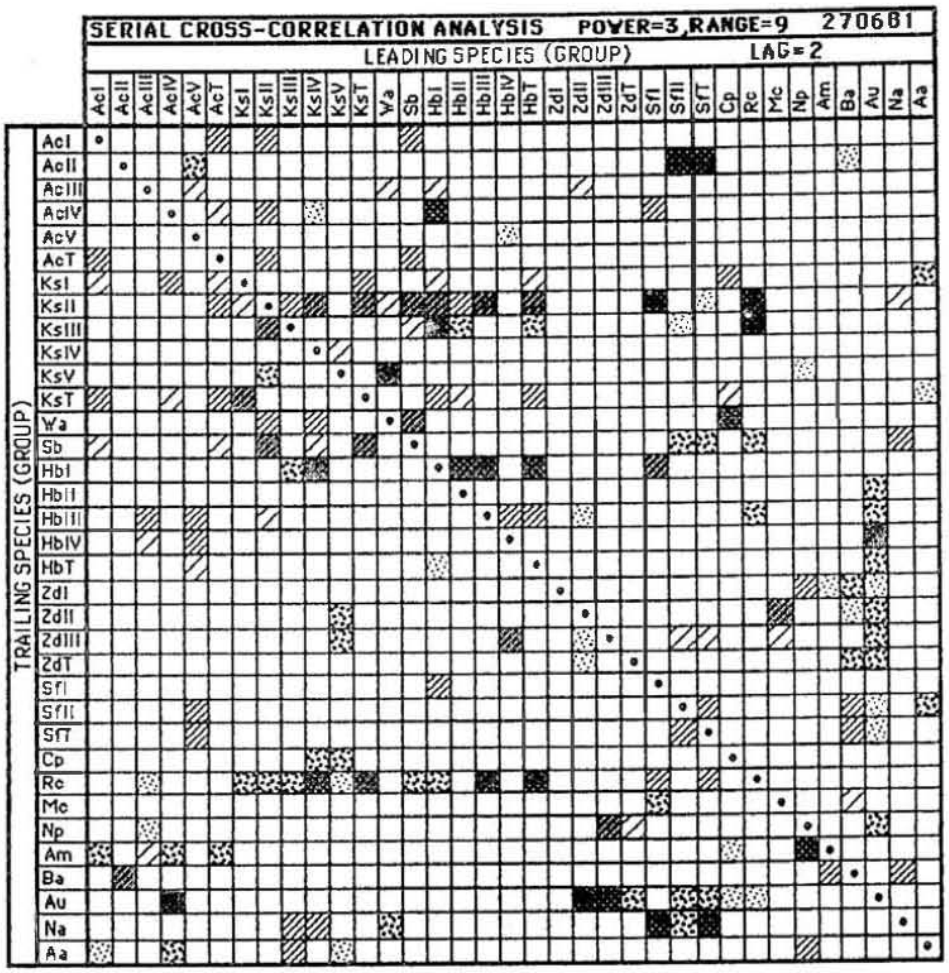

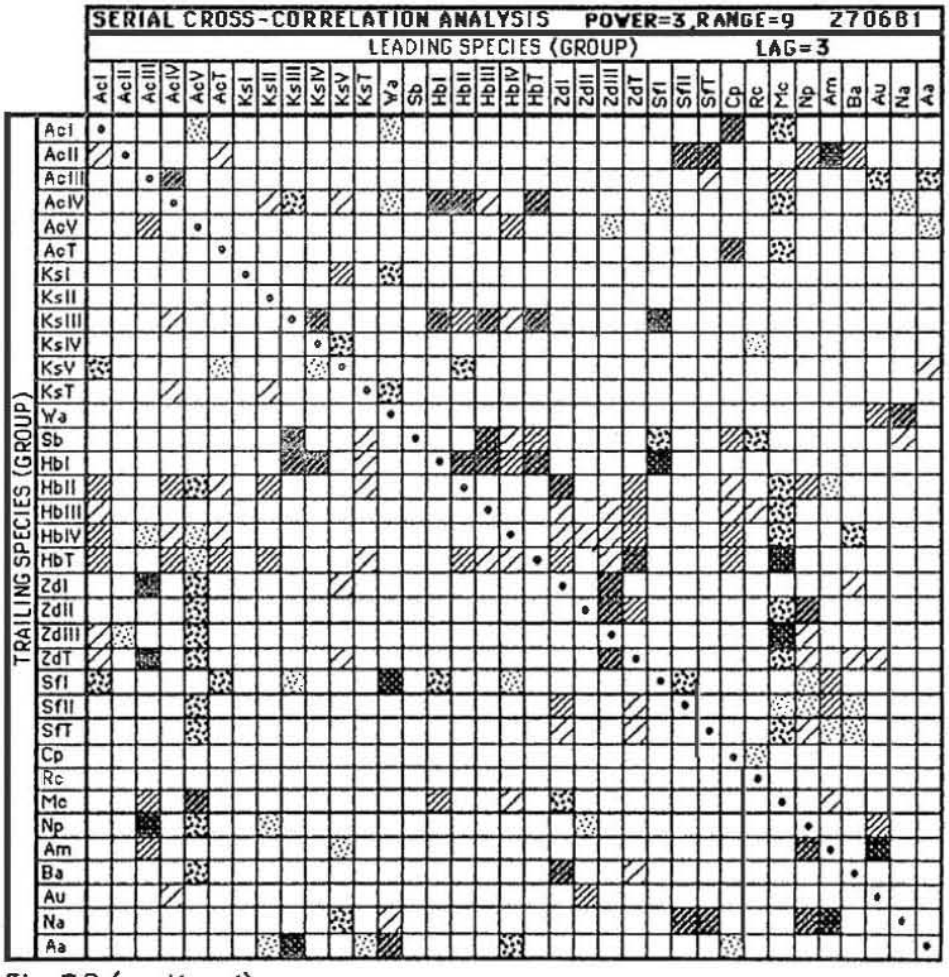

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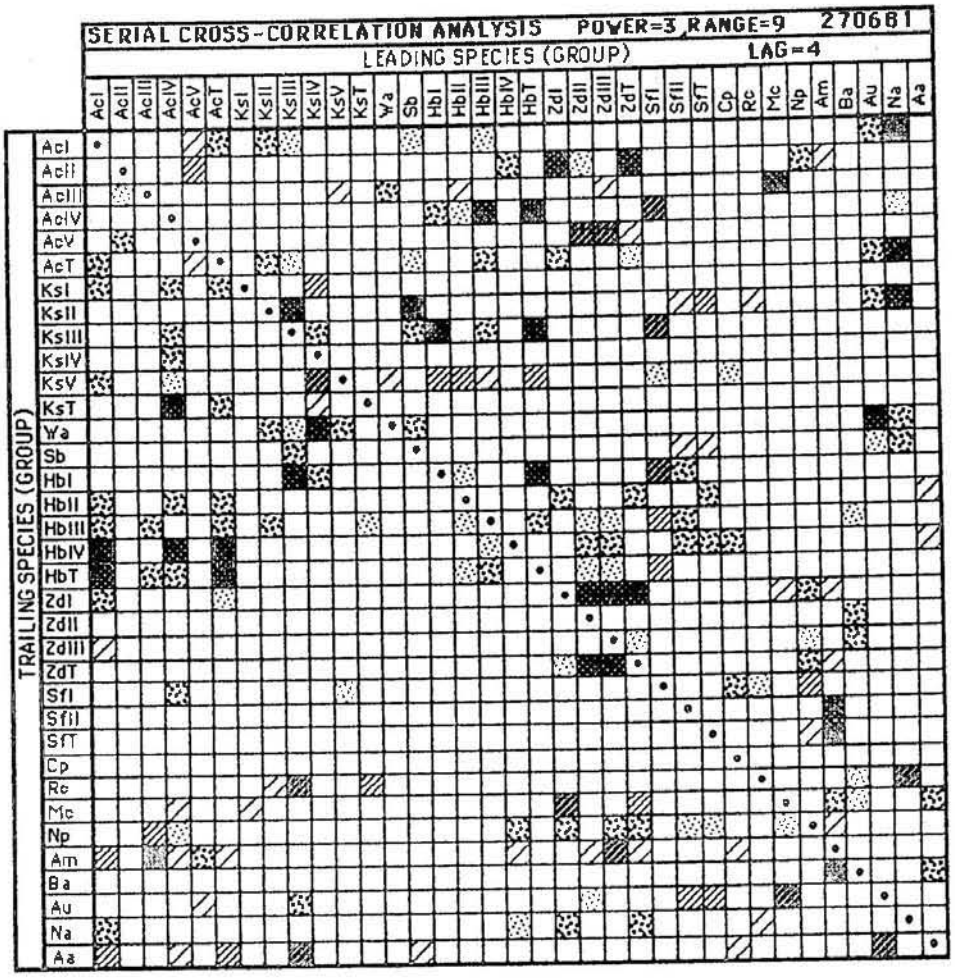

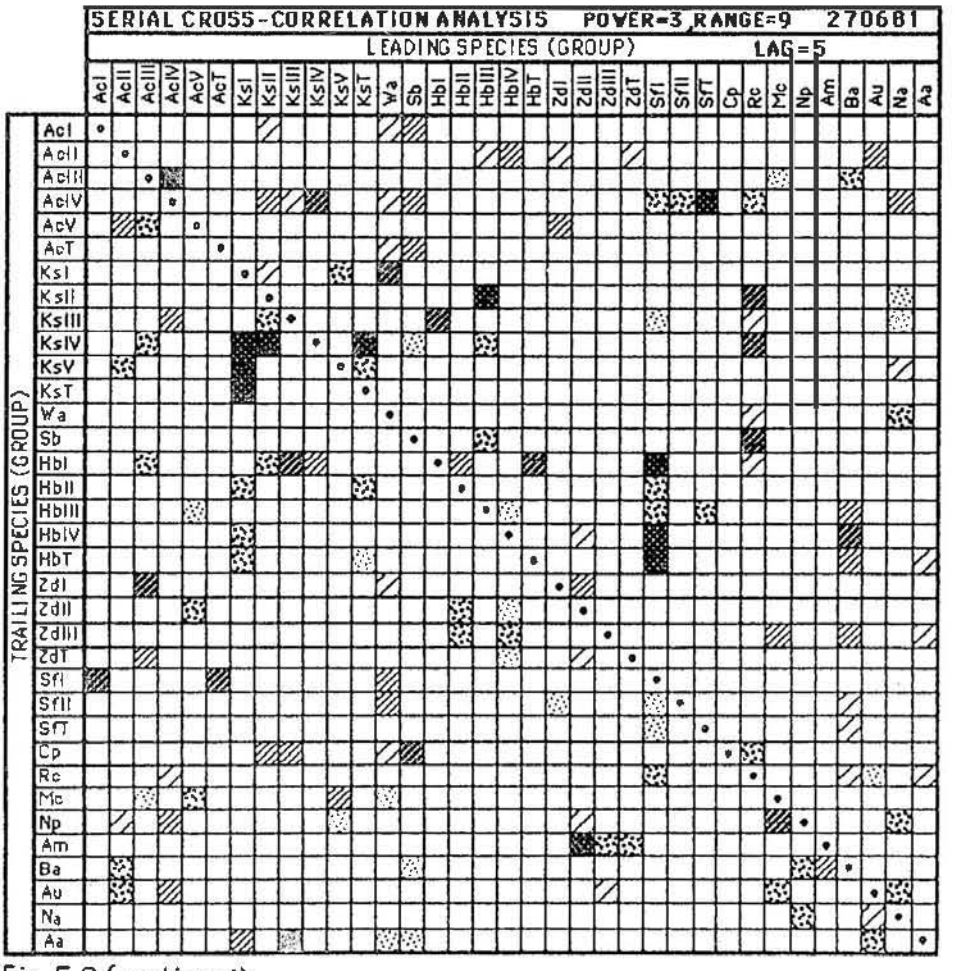

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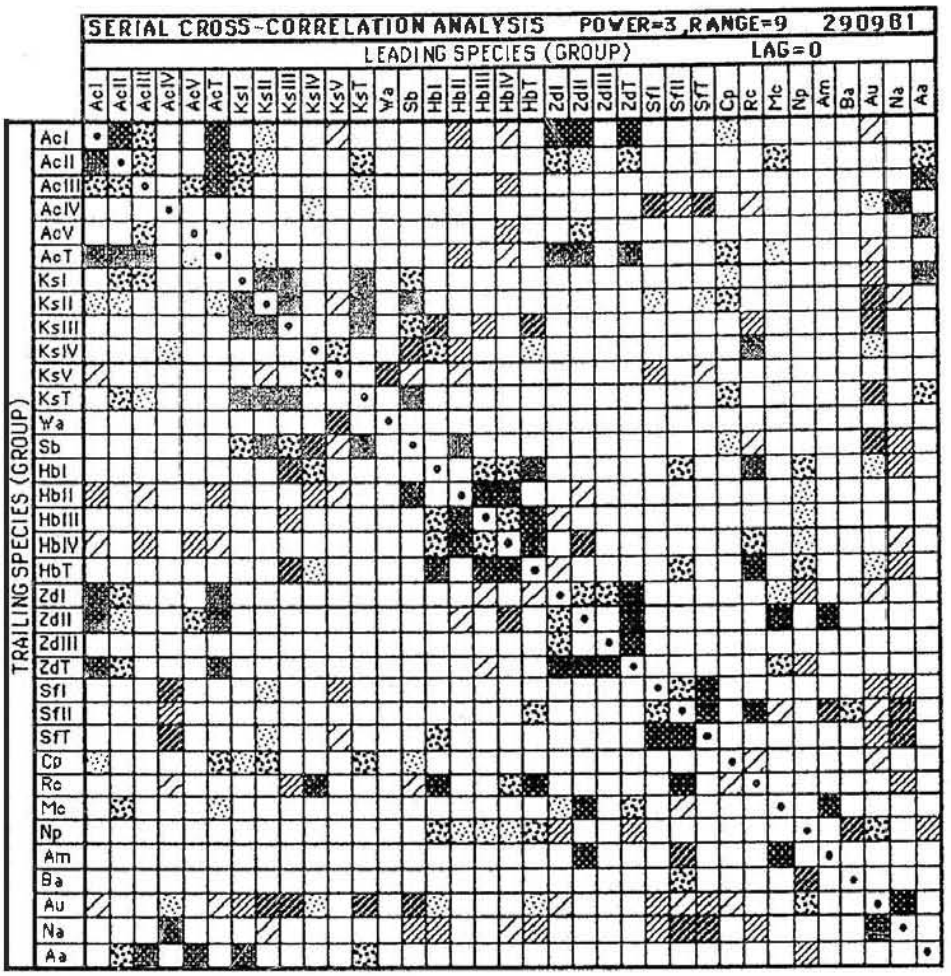

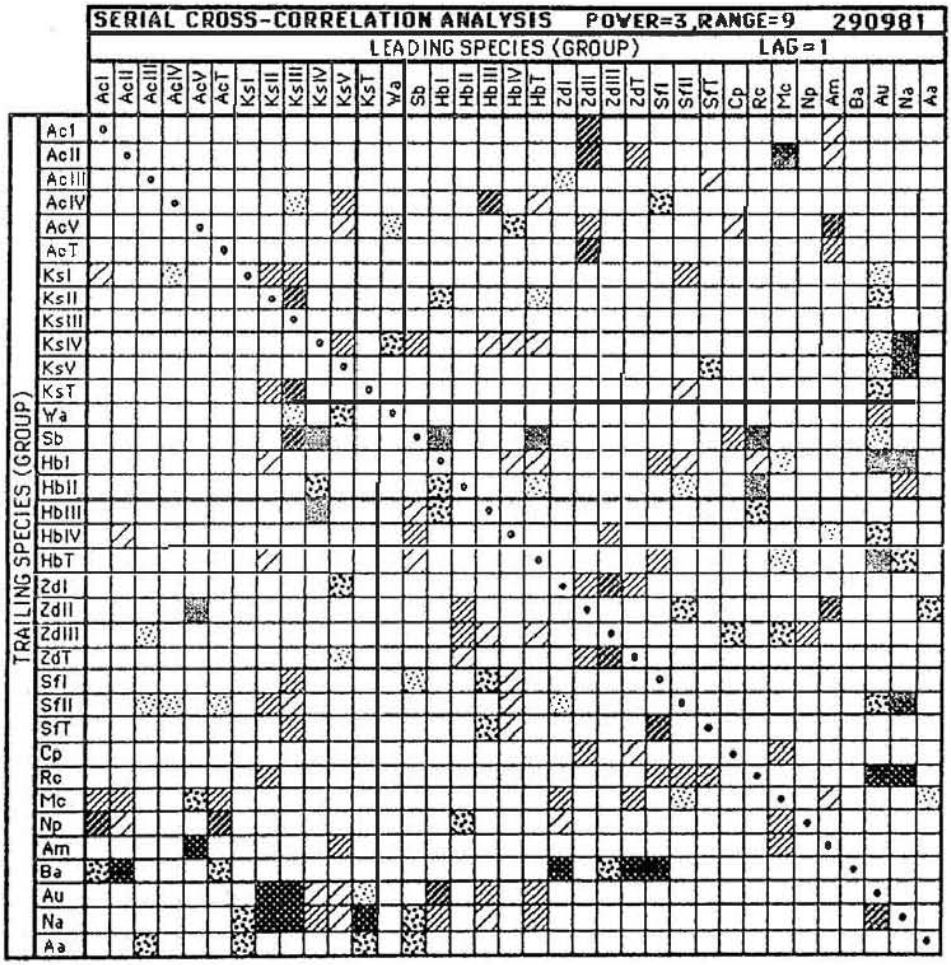

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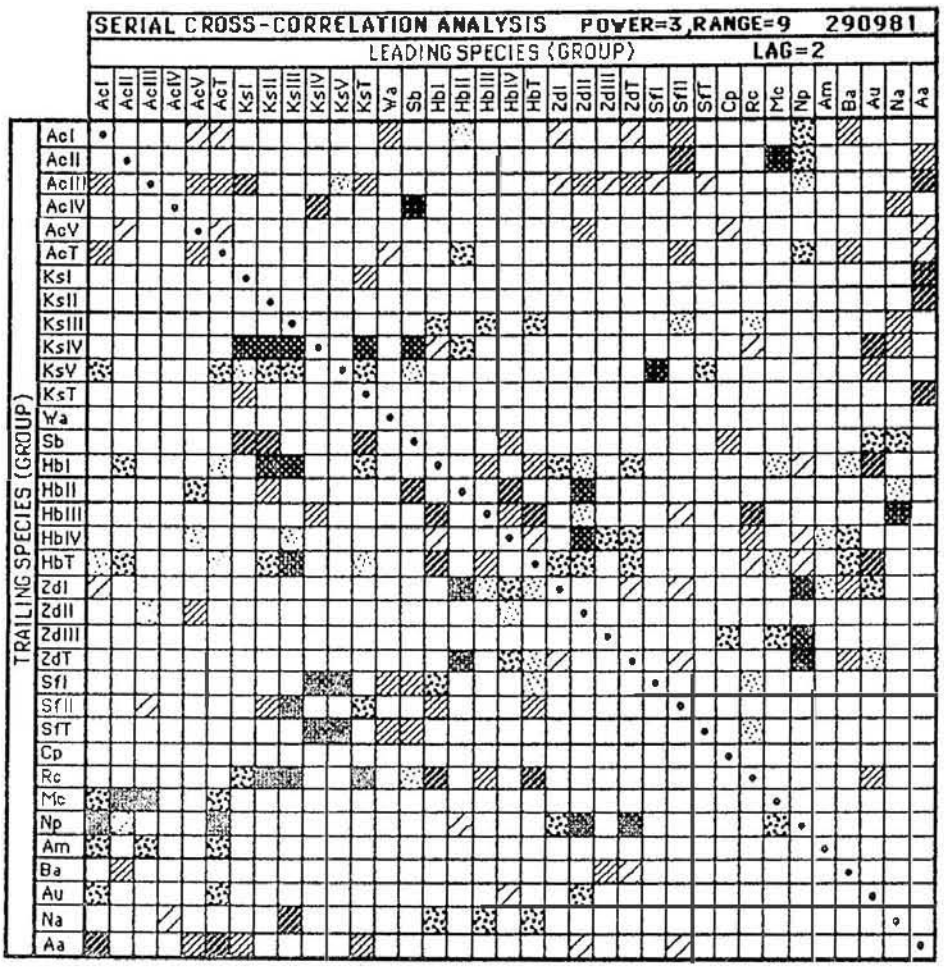

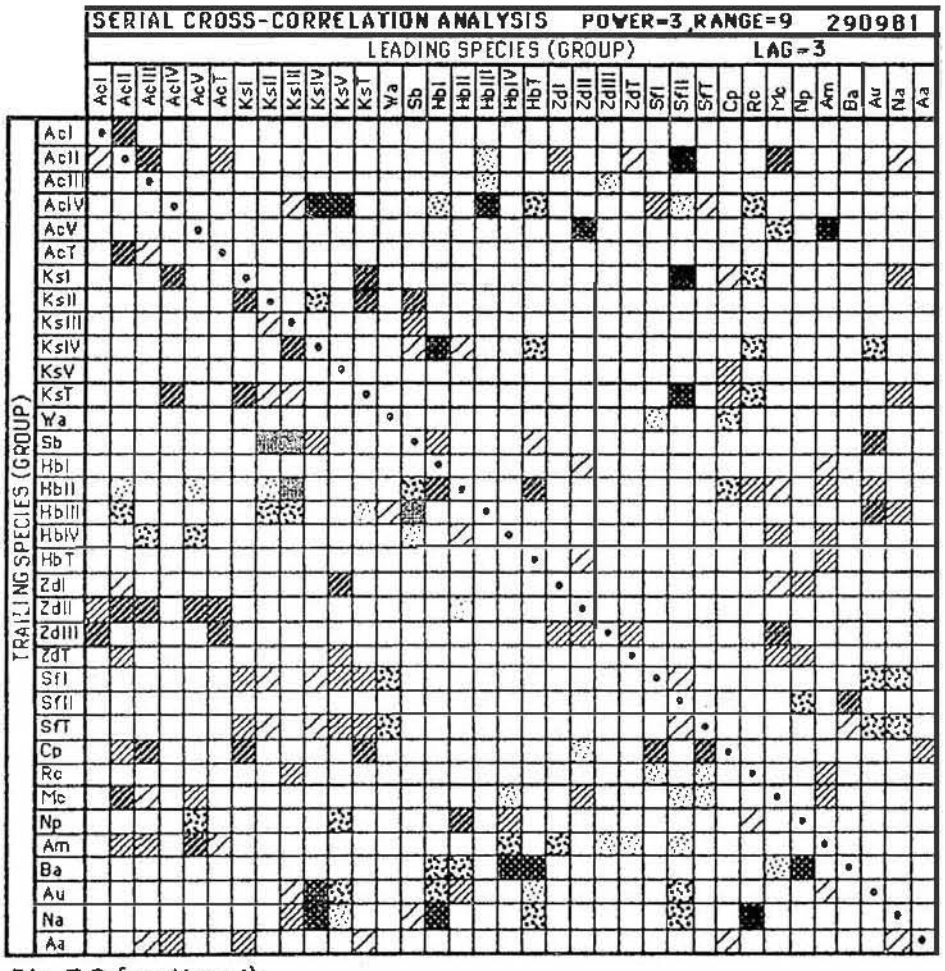

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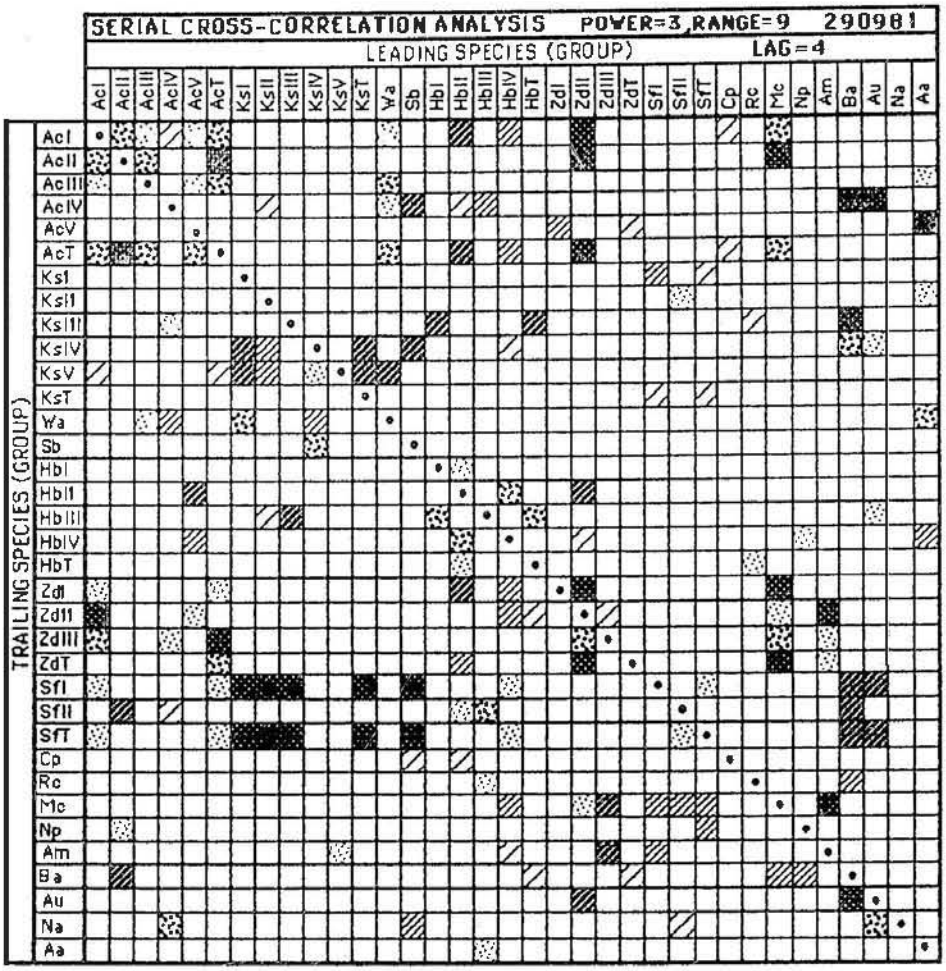

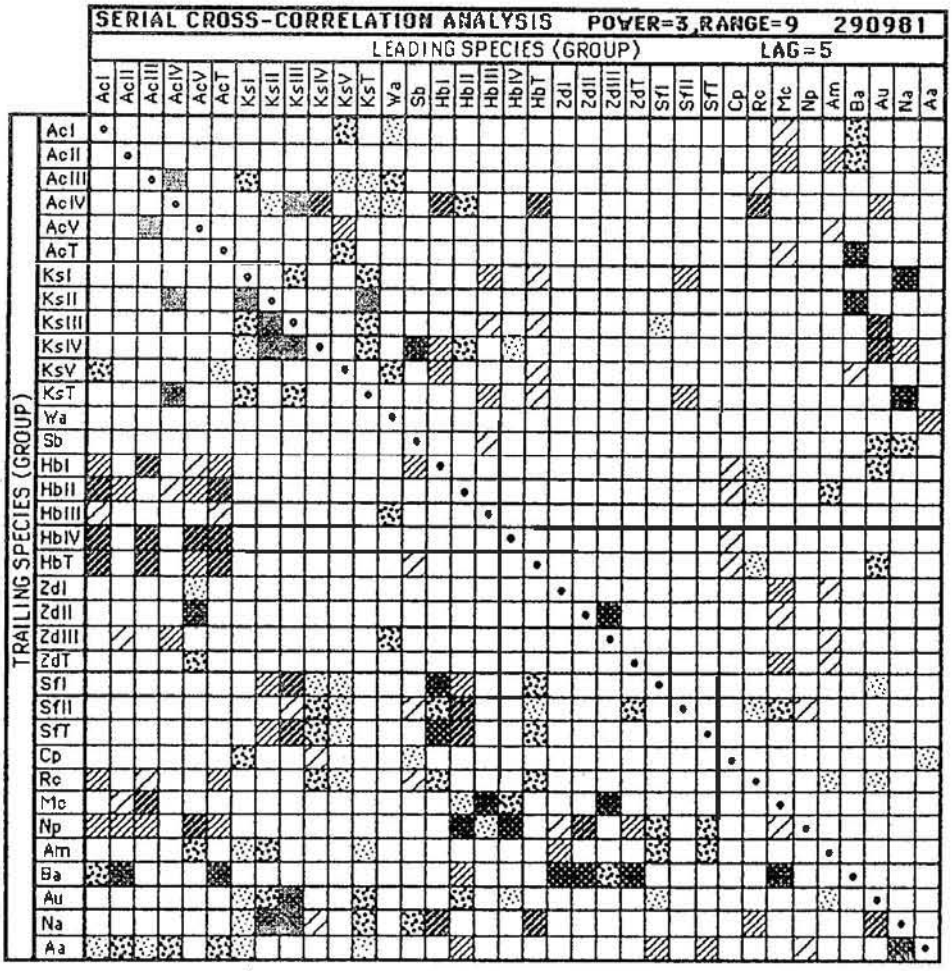

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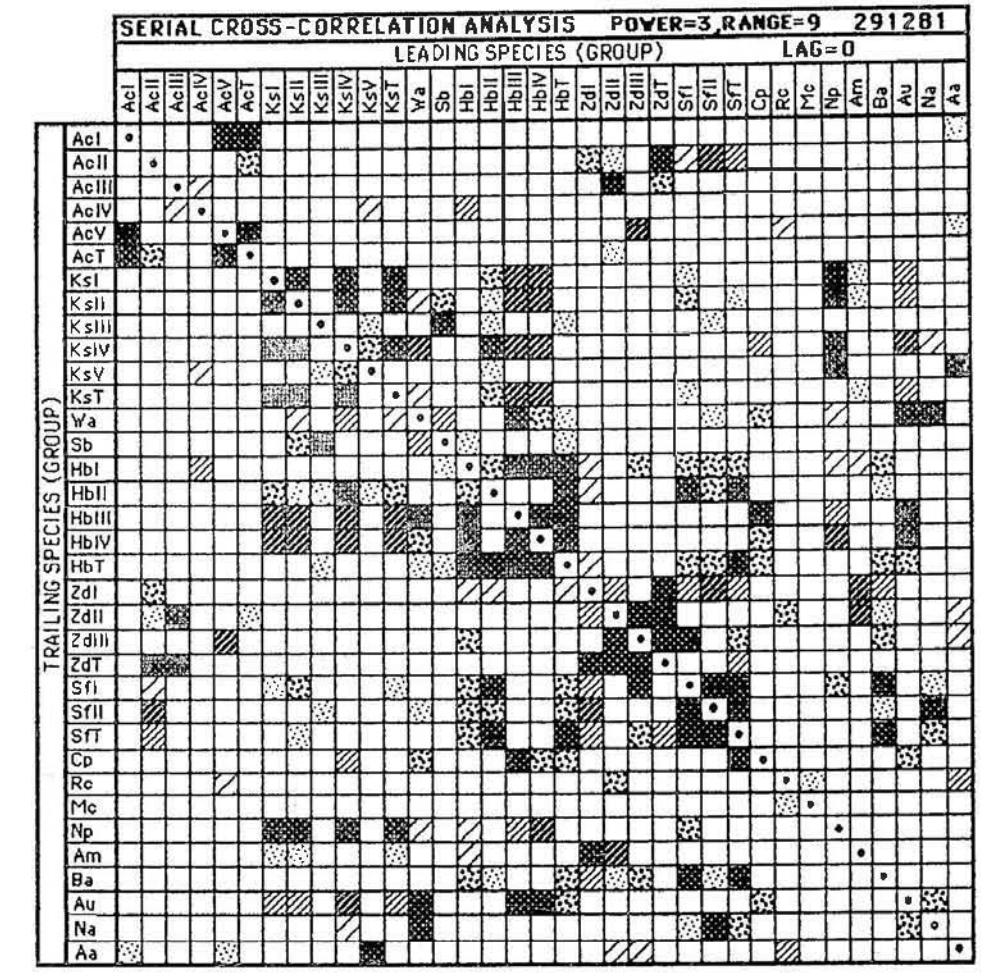

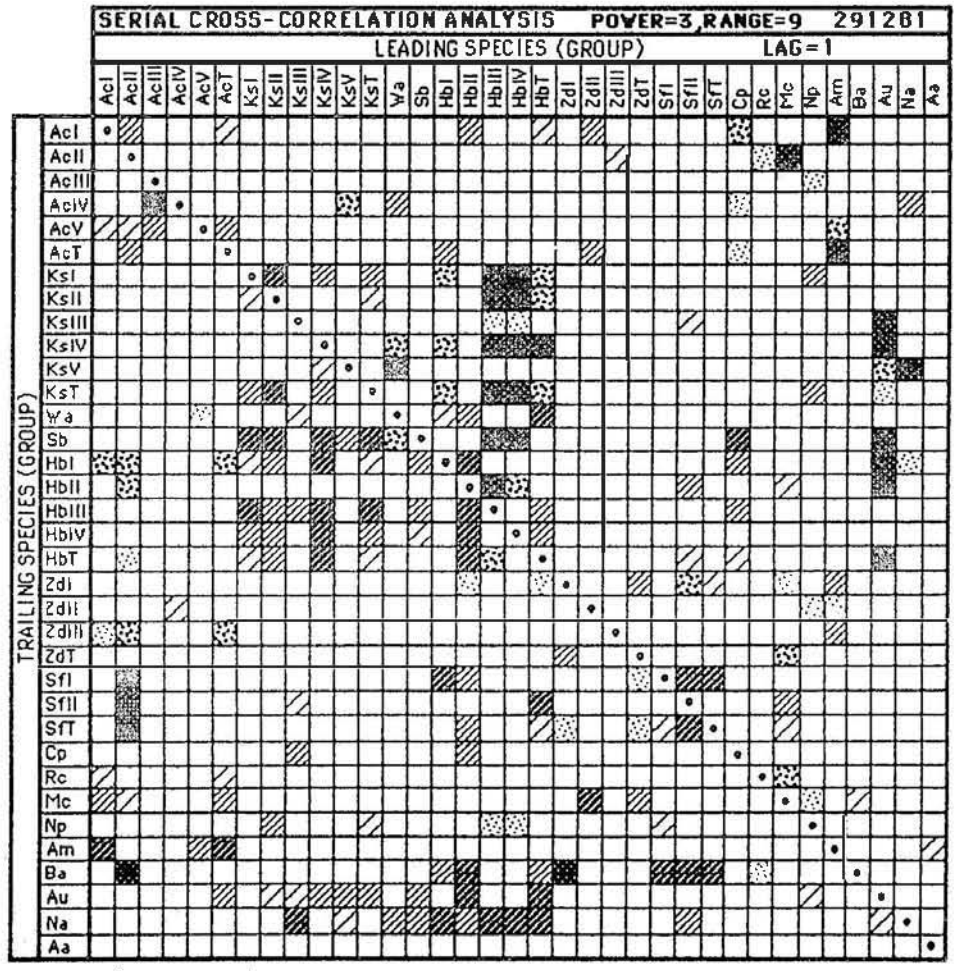

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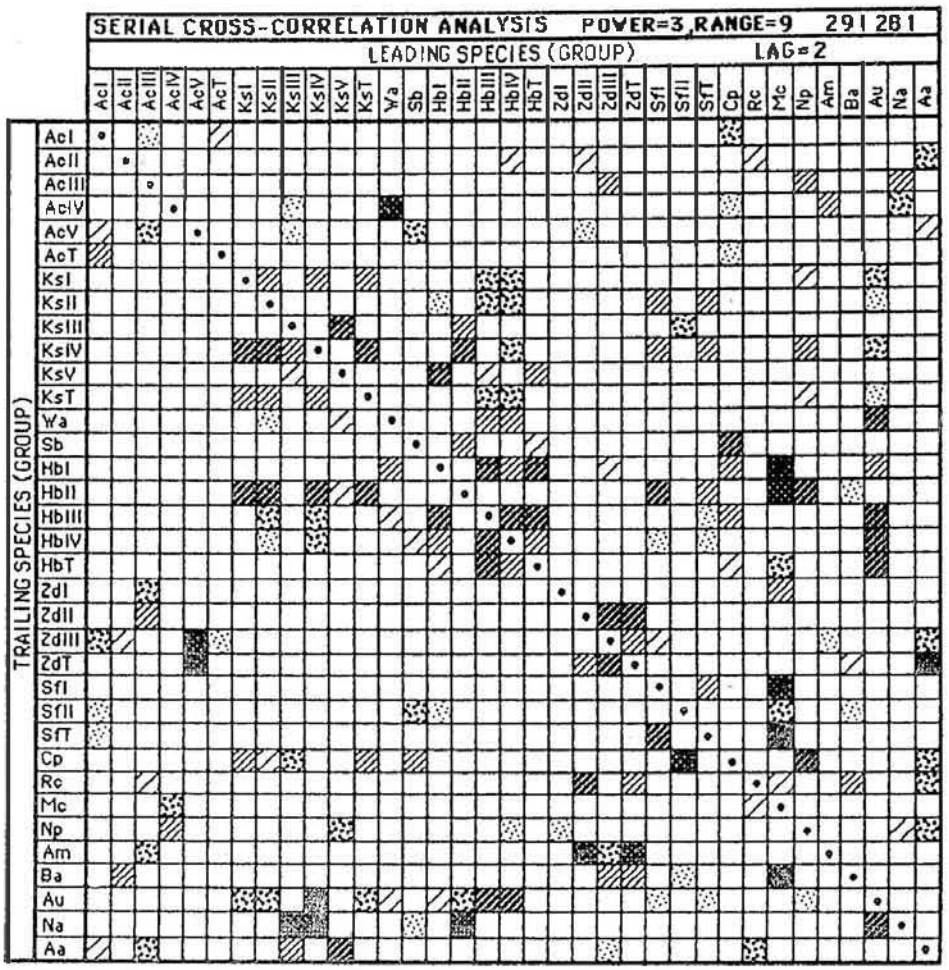

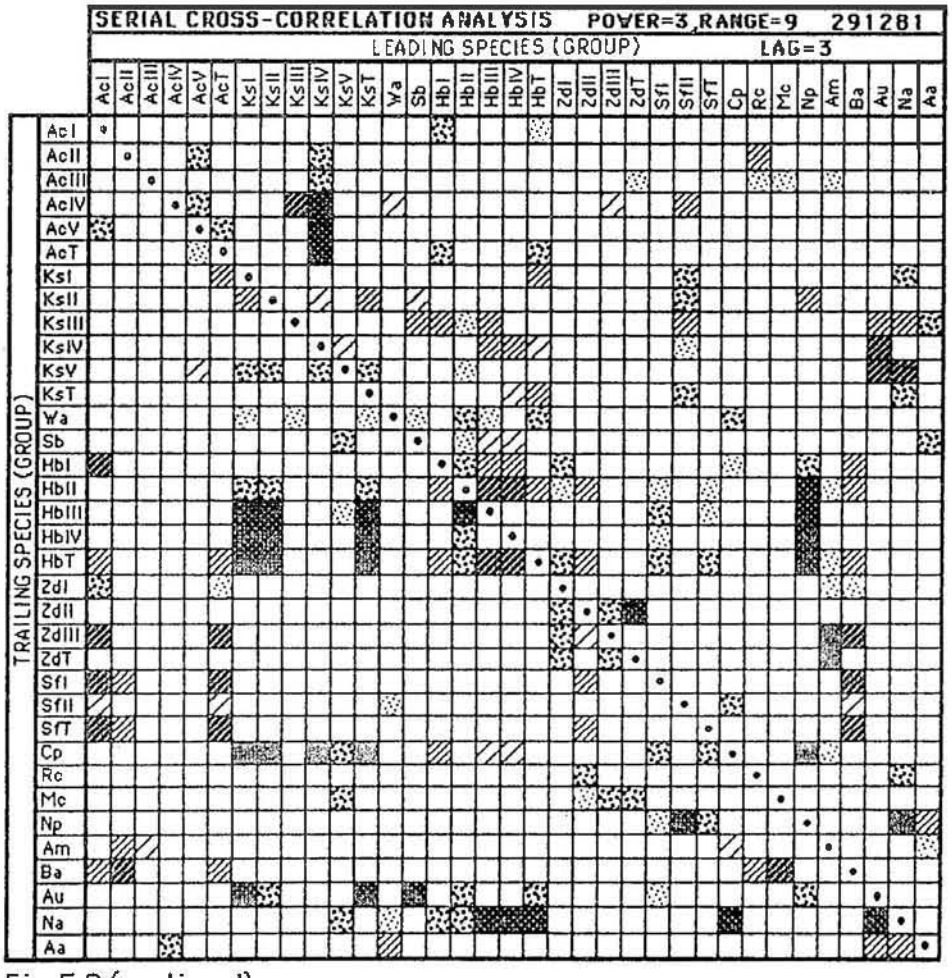

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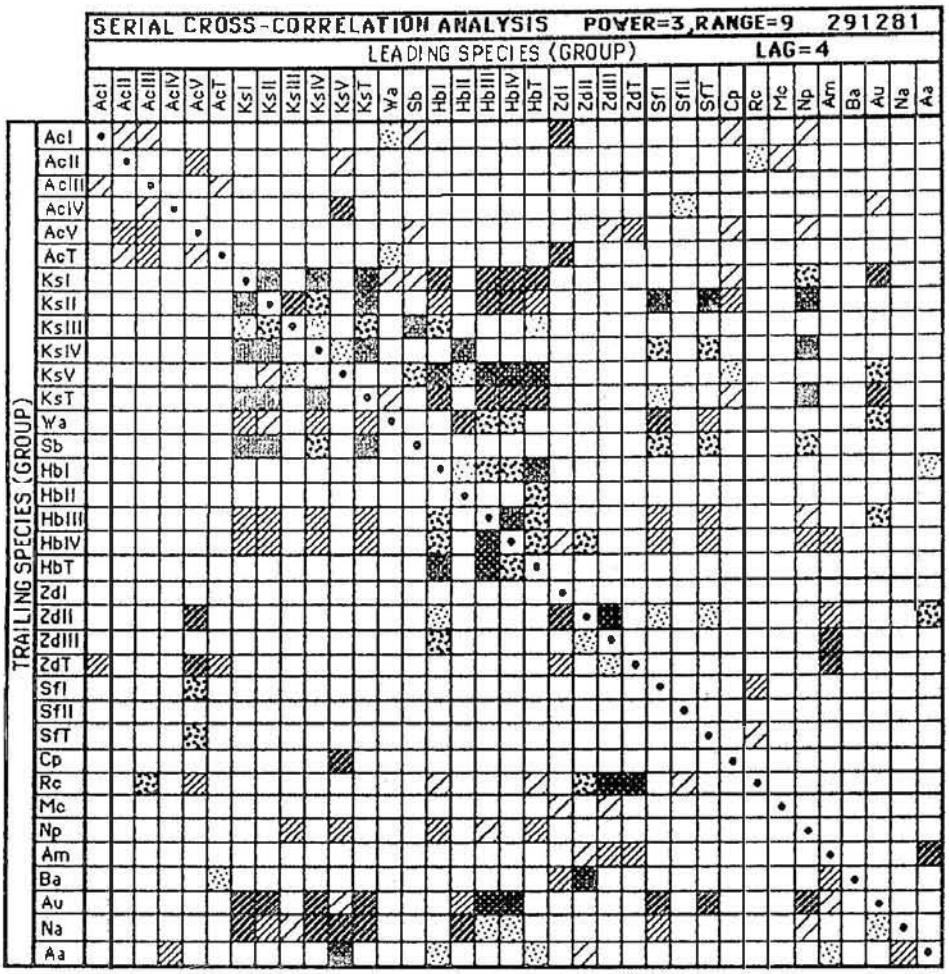

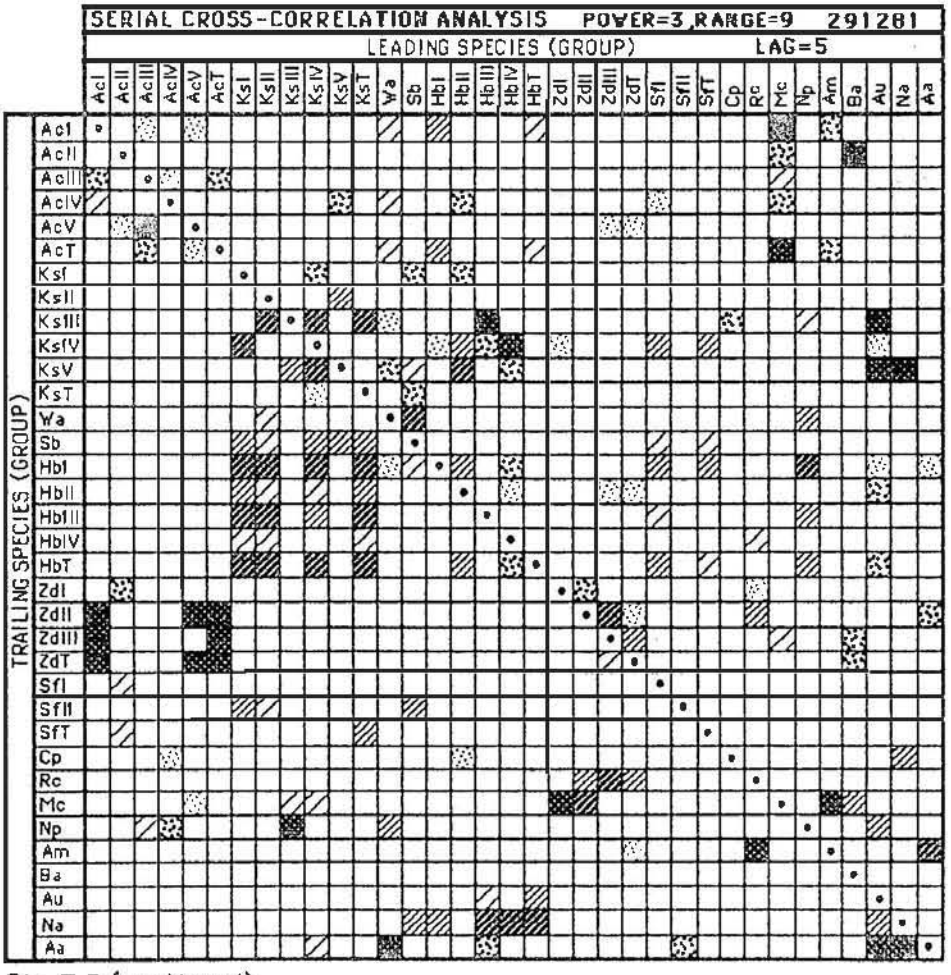

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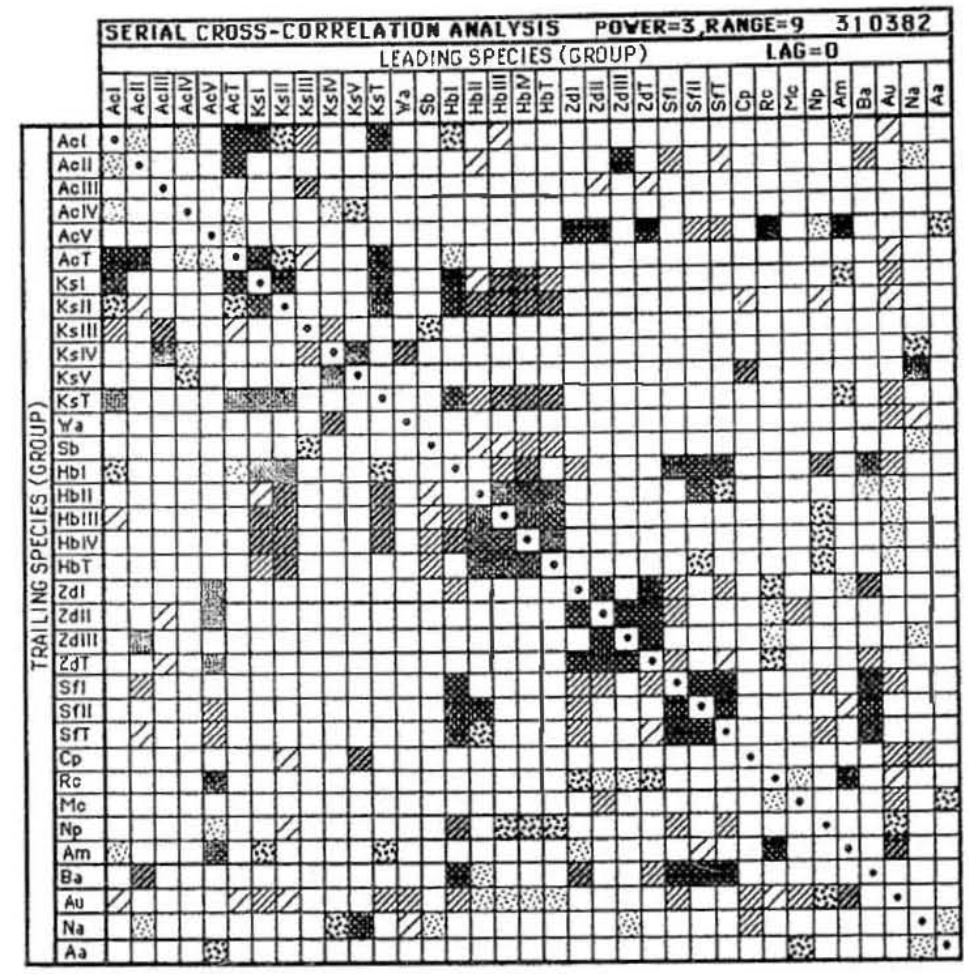

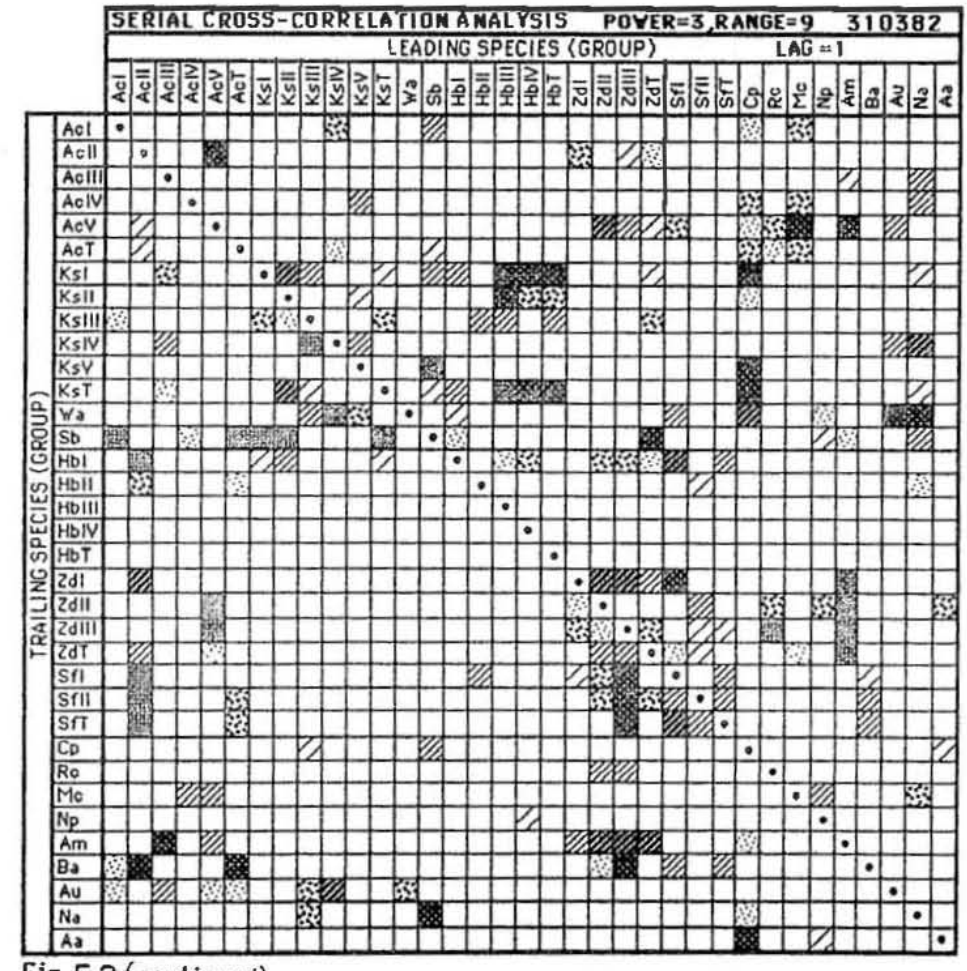

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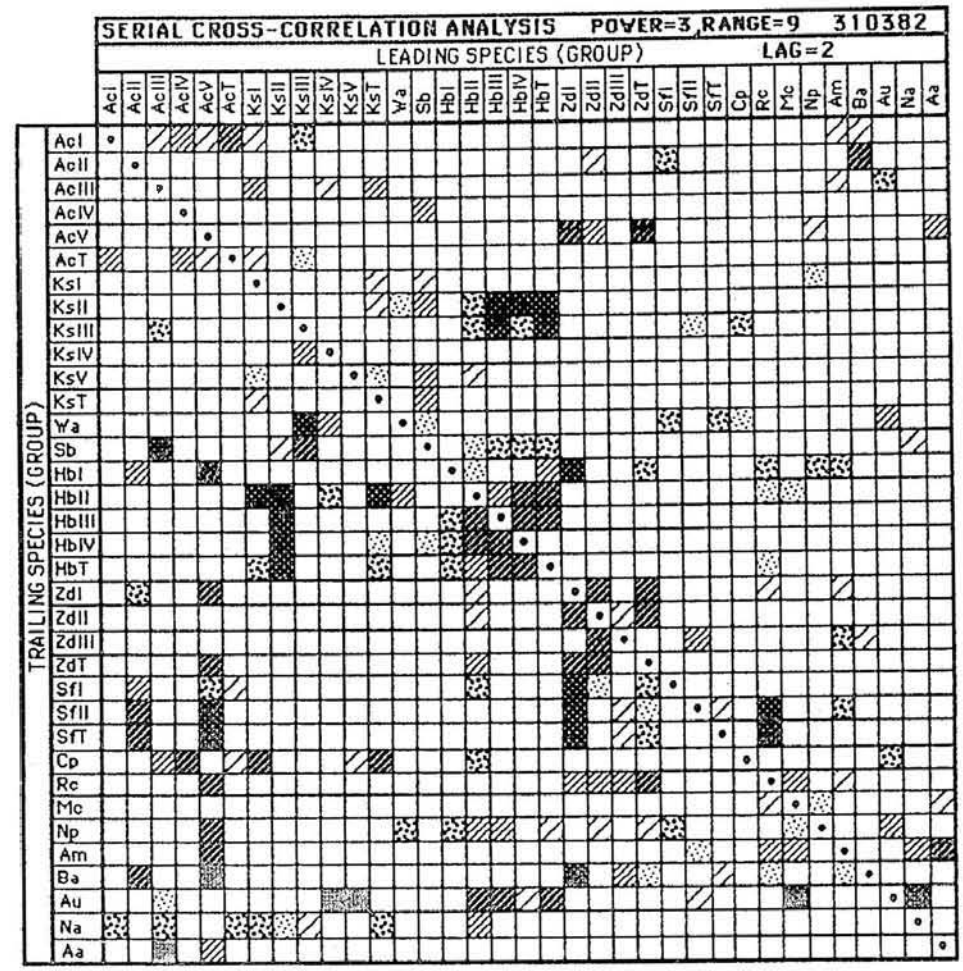

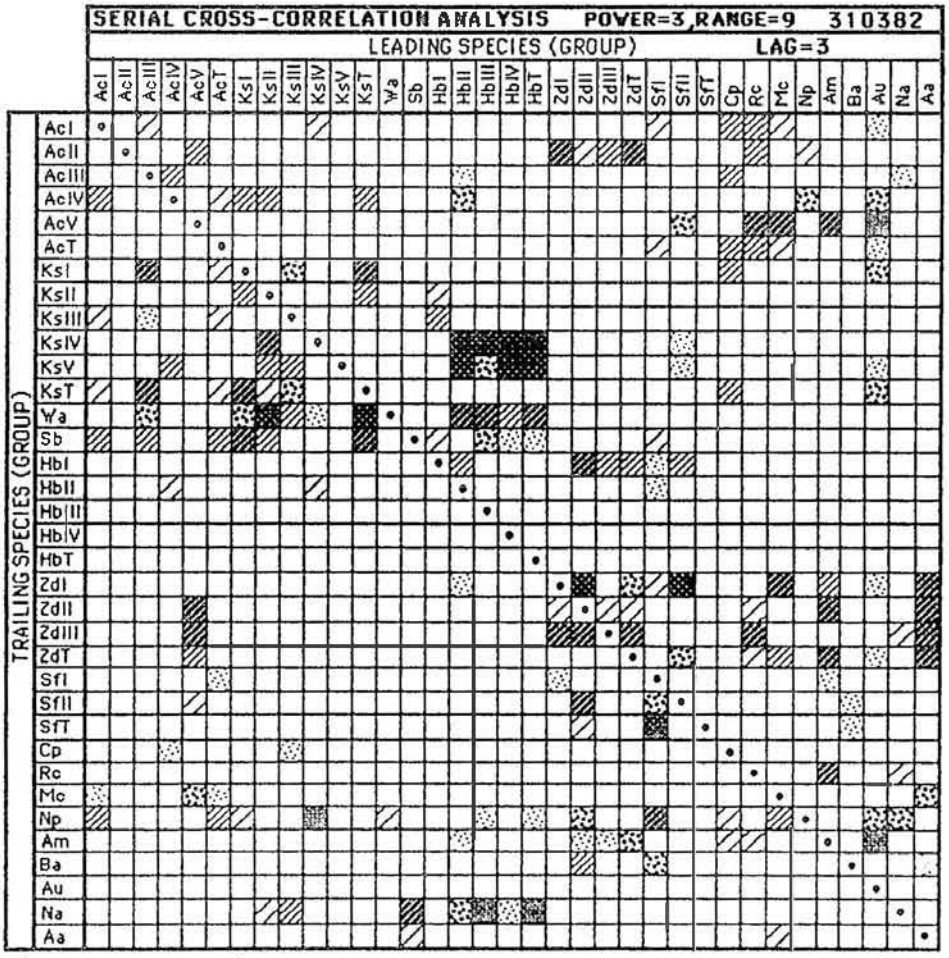

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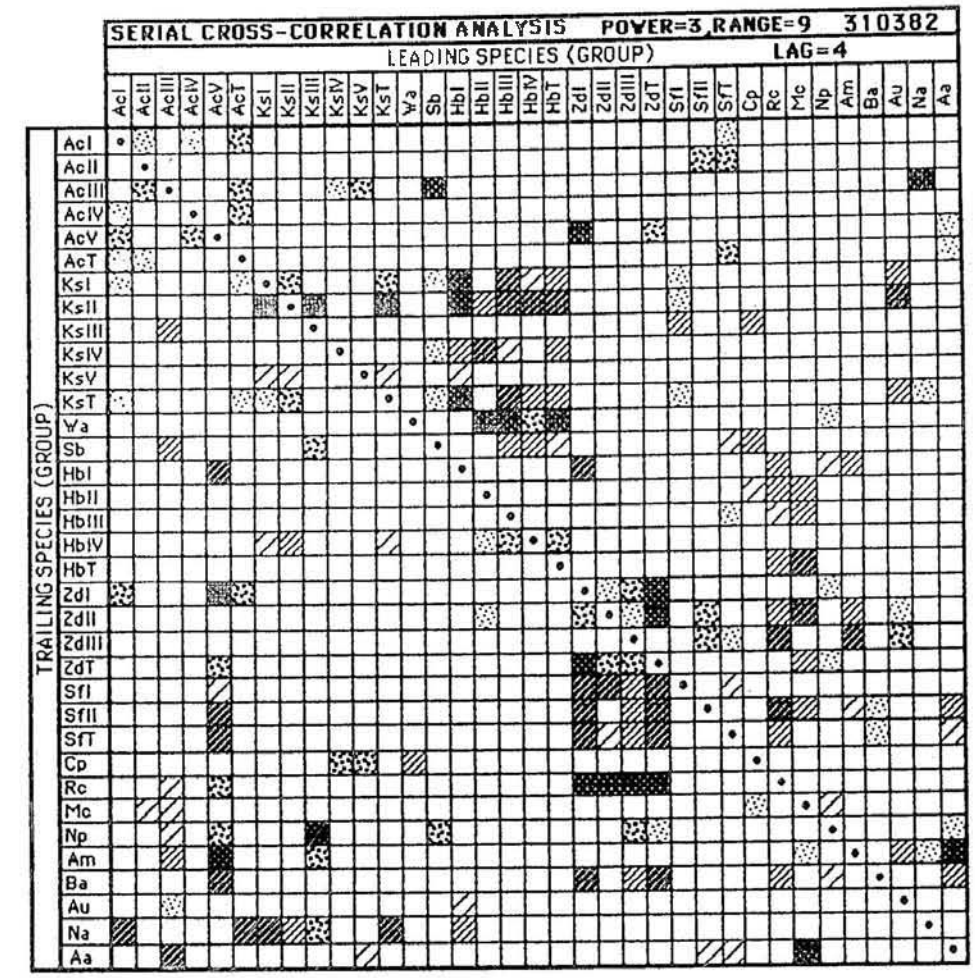


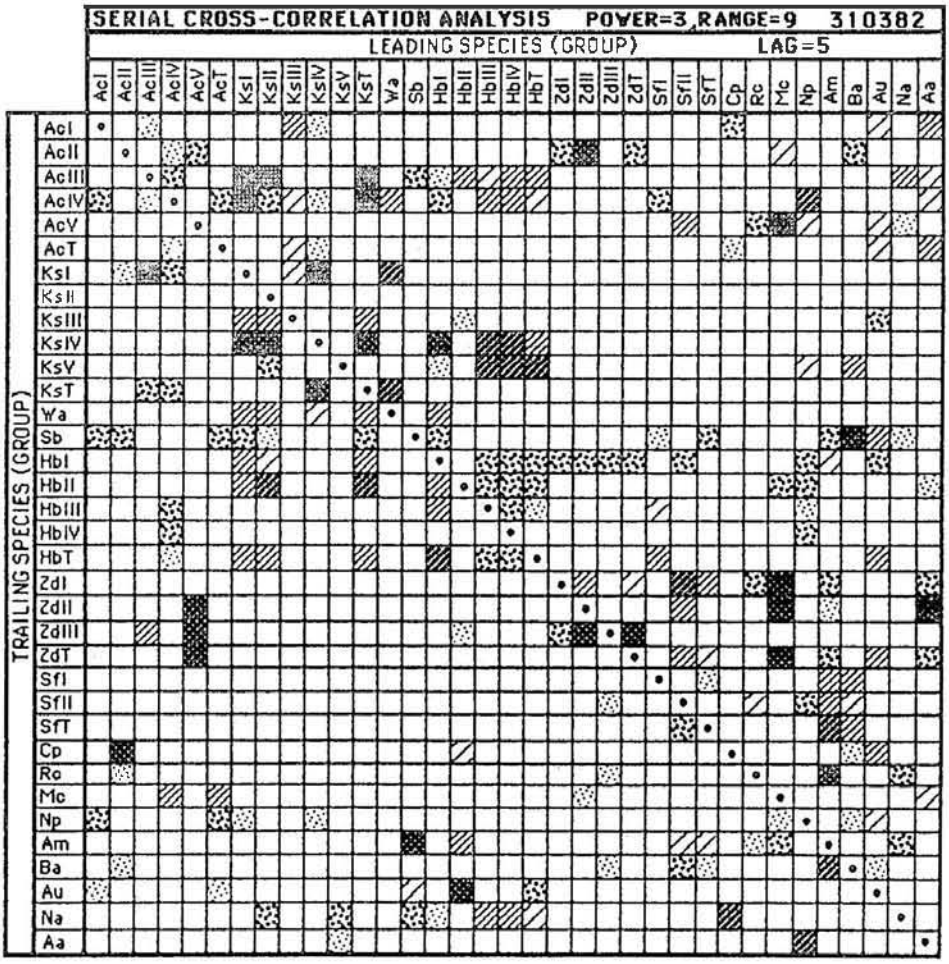


Fig. 5.2 (continued)

trailing series further up the beach. In the calculations, pairwise comparisons between distributions were made with each series being taken as the leading species in turn.

In Fig. 5.2, the correlograms are separated into two halves, above and below the diagonal. To produce the plots, the coefficients above the diagonal were calculated with the top edge groups as the leading series while those below the diagonal were calculated with the left edge groups as the leading series. The species groups at the top of the figure, however, are always identified as the leading groups while those along the left edge are always the trailing groups. Using this notation, the coefficients below the diagonal are equivalent to the correlations calculated after an up-beach shift of the left edge species with respect to the top edge species.

The net result is that the upper half of the correlograms show the correlations between the abundance of a top edge series and the abundance of a left edge series further up the beach. The lower half of the correlograms indicate correlations between the abundance of a top edge series and the abundance of a left edge series further down the beach. Since the cross-correlation coefficient $r_{ij}(k) \neq r_{ji}(k)$ (see Section 5.2.4) it is possible to identify directional relationships between two cross-correlated series.

If there is a real displacement of the series, possibly mediated by biotic interaction, then significant correlations would be expected at non-zero lags. Thus, if one series genuinely tends to displace the other along the beach, negative correlations would be likely at zero and short lags, and positive correlations at longer lags.

If the two series have a mutual (no displacement) positive relationship, they would have strong positive correlations at zero and short lags and (possibly) negative correlations at longer lags. Conversely, a mutual negative relationship would lead to strong negative correlations at zero and short lags and (possibly) positive correlations at longer lags.

Obviously these patterns represent ideal relationships and in practice only approximations could be expected.

General patterns

In all seasons the lag zero correlograms show the greatest degree of significance. By definition, these correlograms are symmetrical about the diagonal and several blocks of significance consistently appear.

All abundant species (*Anapella*, *Katelysia*, *Hydrococcus*, *Zeacumantus* and *Salinator*) typically exhibit interaction between their constituent groups. These species also show interaction with each other and with the less abundant species.

Anapella, for example, frequently has significant correlations with *Zeacumantus*, *Anthopleura* and, to a lesser extent, *Hydrococcus*. *Katelysia* interacts with *Soletellina*, *Wallucina*, *Hydrococcus*, *Cylichnina* and *Anthopleura*. *Hydrococcus* is generally correlated with *Salinator* and *Cylichnina*.

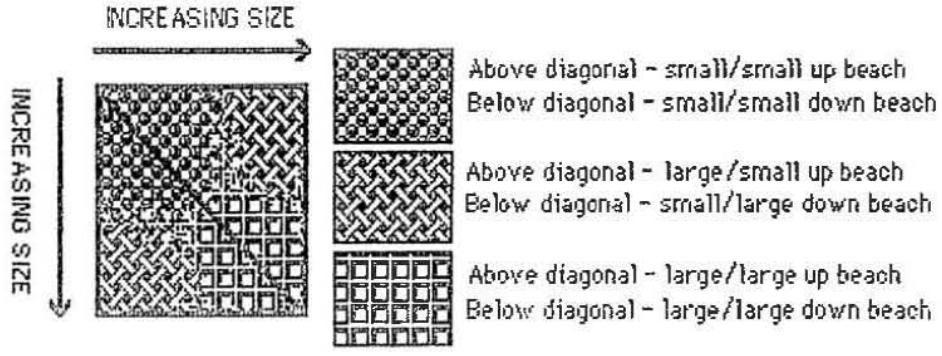
The significance of the above correlations (not necessarily their sign) is loosely transferred among the correlograms of successive lags, although the degree of transferrance differs from season to season, with winter and spring being the seasons of lowest degree. In all seasons there is a considerable loss of symmetry in the non-zero lag correlograms. In general, the correlograms at large lags are more sparce than those at smaller lags but there is no monotonic decline in significance.

5.3.4.2 Between group correlations

The interpretation of the between-group portions of the correlograms will be aided by reference to the generalisations made in Table 5.3. Again, the lack of independence between a species total and its constituent groups negates any strict interpretation of the relevant correlation coefficients. It is neither practical nor useful to describe the correlograms in intimate detail.

As discussed previously, the correlograms represent reductions of the original data sets and are not formal tests of hypotheses. Instead, they allow hypotheses to be generated and they must therefore be examined for general patterns rather than for detailed relationships between all possible group pairings. This is true for both the between-group and between-species pairings.

Table 5.3: Informal interpretation of between-group (within a given species) correlogram block patterns. The diagonal here represents the diagonal of the correlogram. Groups are either 'small' or 'large' and correlations (top/left) are either 'up' or 'down' the beach relative to the top edge groups. Sign of coefficients ignored for the present.



As shown in Table 5.3, the important features of the between-group blocks are the directional relationships between the different size groups; in addition, the sign of the coefficients and the lag-related trends must also be considered. The principal indicator of association, however, is always the lag zero correlogram.

Anapella

On 200381 groups I and III and groups II and IV are negatively and positively correlated, at lag 0, respectively. With increasing lag most correlations are in the down-beach direction. Group I, in particular, is correlated with larger groups at short down-beach lags; the larger groups have similar correlations amongst themselves. Most coefficients are positive at short lags and negative at longer lags; also, at longer lags correlations are weaker. These patterns indicate a relative separation of small and large animals, with the smaller animals being correlated with the number of larger animals further down the beach.

There are fewer significant correlations between *Anapella* groups in winter (group I, in particular, has greatly reduced correlation). At lag zero they are positive between a representative range of groups. Unlike the previous season, there is approximately equal directional correlation at non-zero lags and no definite alternation of sign or decrease in significance with increasing lag. Also, the general trend is for the numbers of the smaller animals to be related to those of the largest group further up the beach. The relationships between more closely sized groups are often in the opposite direction.

In spring, the sign of the correlations changes from positive at lag zero, through negative at lags 2 and 3 to positive again at lags 4 and 5. The lag 0 and 4 patterns are very similar, with correlations ocurring between groups I, II and III (in both directions). There are no consistent directional correlations between any groups in this season.

There is also a general alternation of sign among the 291281 coefficients. The sign changes from being mostly negative at lags 0 and 1 through positive at lags 2 and 3, negative at lag 4 and finally positive at lag 5. At lag 0 groups I and V are positively, and groups III and IV, negatively related. The smaller animals tend to be correlated with the largest group's numbers down the beach. The smaller groups are most often correlated with each other in an up-beach direction.

In the 310382 autumn the coefficients are negative at lags 2 and 3 but otherwise positive. At lag 0 group I is associated with groups II and IV. Unlike the previuos autumn, there is no decrease in the significance of the correlations with increased lag. Also, the

intermediate groups are often correlated with smaller animal numbers further up the beach.

In summary, winter appears to be the season of least interaction (along the transect) between *Anapella* groups. Autumn and spring are similar in that many groups show strong positive relationships at short lags. In summer, by contrast, the short lag correlations are negative. The most marked interactions are between the smaller and larger groups. While the abundance of small animals is related to that of large animals up the beach in winter, in summer this relationship tends to be in the opposite direction. This may be related to the reservoir of breeding adults, suggested in Chapter 3, between similarly sized groups, the correlations are often down the beach.

Katelysia

Katelysia exhibits substantially more interaction between its groups than *Anapella* does and correlations are strongest in summer.

In the 200381 autumn group III is negatively correlated with both small and large groups at lag zero (it is in this season that group III is most abundant). Also at lag 0, group I and the large groups are positively associated as are the larger groups amongst themselves. There is a cyclic pattern in overall interaction, with lags 0, 2 and 4 being considerably more active than legs 1, 3 and 5. At non-zero legs the interactions between pairs are often significant in both directions, a feature not found with *Anapella*. There are no well defined changes in the sign of the coefficients with increasing lag.

Unlike the previous season, the interactions between a given pair at a given lag in winter are typically unidirectional. Also, there is no evidence of a cyclic pattern in the overall correlation strength. Again, however, there are no clearly defined changes in the sign of the coefficients although negative coefficients occur mostly between similarly sized groups. At lag 0 positive correlations are evident between group I and groups II and V and between group IV and groups III and V. No pairings have consistent relationships at non-zero lags.

In spring the previously loosely structured correlograms are replaced by plots having both sign alternation and consistent relationships between a limited number of pairs. At zero lag most relationships are positive and are strongly so between groups I, II and III and between groups IV and V. There is a general alternation of sign at successive lags. At lag 1 the above groups are significantly correlated in the up-beach direction. For subsequents lags, however, the number of small animals is related to the abundance of larger animals down the beach. Also at these lags, there are minimal correlations between groups I, II and III. Instead, there general pattern is for those groups to be correlated

with the larger groups IV and V.

An alternation of sign remains in summer but the trend is somewhat broader. Positive coefficients at lag 0 are followed by negative terms at lags 1 and 2, positive terms at lags 3 and 4 and negative terms at lag 5. Again, the majority of correlations are in the between small groups and large groups down the beach. At lag 0 there is comparatively little interaction between groups I, II and III but these groups are correlated with groups IV and V. These generalisations also apply to the non-zero lags.

The 310382 autumn shows a return to correlograms similar to those of the previous autumn, with some exceptions. The smaller and larger groups tend to be positively associated at lag 0 while group III is negatively correlated with group IV. There is a general tendency for correlations to be down the beach at non-zero lags. There is no defined alternation of sign and there is also evidence of bidirectional correlations, particularly between the smaller groups.

To summarise, zero lag correlations are typically positive in all seasons except for those involving group III in both autumns. In autumn the correlograms are loosely structured, often with bidirectional correlations. Over winter the interactions become more unidirectional. The small group abundances are related to the large group abundances down the beach in spring and summer. There is then a strengthening of the interactions, as evidenced by the development of sign alternation between successive lags. Most significant correlations occur between small and large groups although in spring there is considerable interaction between the smaller groups.

Hydrococcus

At zero lag on 200381 groups I and II are negatively, and groups I and III and II and IV, positively correlated. At non-zero lags many of the interactions between pairs are bidirectional. Most significant correlations involve either group II or group III but no definite trends exist.

Very strong lag zero interactions occur in winter with all groups being positively correlated. There is then a marked alternation of coefficient signs with increasing lag as the overall strength of the correlations diminish. Almost all correlations are unidirectional with the numbers of large animals being related to the numbers of smaller animals up the beach.

There is again strong positive interaction between most groups at zero lag in spring. Correlations decrease rapidly with increasing lag, however. While lags 0, 1 and 4 have positive coefficients, lag 2 and 3 terms are negative; lag 5 has no significant correlations. No consistent directional trends are evident.

No regular alternation in sign occurs in summer and at most lags the correlations are generally bidirectional. Lag zero correlations are again strong and positive between most groups. At other lags the significant correlations usually involve group I and/or group II. In the 310382 autumn correlations involving group I are negative at lag 0, otherwise they are positive at that lag. There is considerable bidirectionality at non-zero lags and, as before, no sign alternation is evident.

Unlike the bivalves described previously, interactions between the *Hydrococcus* groups weaken considerably with increasing lag in most seasons. Also, the correlations are typically bidirectional and show no regular alternation of sign. The exceptions occur in winter when large animals are strongly correlated with small animals further up the beach and when is sign alternation, indicating strong interaction over short distances. In both autumns group I exhibits evidence of negative correlations with other groups at zero lag; otherwise most groups are have strong positive associations at that lag.

Zeacumantus

Zeacumantus is similar to *Hydrococcus* in that its correlograms show considerable bidirectionality. Also, there is typically strong positive interaction between the groups at zero lag (particularly so in winter); in summer groups I and II are negatively correlated at that lag.

The 200381 autumn is characterised by a strong positive correlation between groups II and III at lag 0. These groups have mutual negative up-beach correlations at lag 1 but no correlations thereafter. In winter large animals tend to be correlated with smaller animals up the beach and there is also evidence of sign alternation between successive lags. This continues in spring but there is then little directional bias. The negative correlations between groups I and II in summer are associated with loosely structured correlogerams at non-zero lags. The 310382 autumn correlograms, however, exhibit numerous correlations at all lags. Many of these are bidirectional and there are generally positive coefficients at lags 0, 4 and 5 and negative terms at other lags.

The above results suggest that *Zeacumantus* groups typically have positive associations over short distances. There appears to be a general trend for an increase in that interaction from autumn to winter (when correlations tend to be up the beach) followed by a decline through spring to a minimum in summer. In fact, in summer the two smallest groups tend to separate out over the distribution transect. There is a return to strong associations the following autumn.

The discrepancy between the two autumn correlograms may be due to extraneous

factors. The 200381 correlograms weaken rapidly after lag 1, indicating interactions persist over only short distances. This may be mediated by the algal mats which were prevalent during that autumn in the distributional zone of *Zeacumantus* and which have strong associations with those animals (see Section 5.3.1).

Salinator

There is little association between the two *Salinator* groups in any season. Correlations are minimal in the 200381 autumn and the winter but are positive at zero lags in other seasons. In summer and the following autumn, significant correlations are also evident at lag 1, indicating the relative strength of the associations in those seasons.

5.3.4.3 Between species correlations

Anapella and *Katelysia*

200381: Only group II shows associations (positive) with the other abundant bivalve, *Katelysia* (smallest and largest groups) at lag 0. There is minimal correlation between *Anapella* and *Katelysia* at non-zero lags.

270681: Group II *Katelysia* animals are positively correlated with *Anapella* groups I and III at lag 0. Small *Anapella* are correlated with large *Katelysia* in both directions at short lags but mainly down the beach at longer lags. Small *Katelysia* are mainly associated with small and large *Anapella* up the beach. At most lags large *Katelysia* are correlated with the medium *Anapella* animals up the beach, while medium *Anapella* are dependent on large *Katelysia* down the beach only at the longer lags. Coefficients are mostly positive, except at lag 2.

290981: At lag 0 *Anapella* groups I, II and III are positively associated with *Katelysia* group II and both small and medium *Anapella* are positively correlated with large *Katelysia*. Most significant correlations occur between large *Katelysia* and medium *Anapella* further up the beach. Coefficients are negative at lags 1 and 2 but usually positive at other lags.

291281: Summer is the season of least interaction overall between *Anapella* and *Katelysia*. Correlations are negligible at zero lag and the few correlations at non-zero lags are typically between large *Katelysia* and medium *Anapella* up the beach.

310382: In the 310382 autumn strong negative correlation occurs between the two species at lag 0 for the first time; this is between group III of each species. Also at that lag, juvenile *Anapella* are positively associated with small *Katelysia* as are large *Katelysia* and medium *Anapella*. At non-zero lags the two species show considerable associations between a variety of size groups. Thus, *Anapella* is generally correlated

with *Katelysia* down the beach and *vice versa*.

Wallucina

200381: Juvenile *Anapella* are negatively correlated with *Wallucina* at lag 0 but with larger animals the relationship is positive. Similar relationships, but of opposite sign, occur at lag 1. At larger lags the general trend is for *Wallucina* to be correlated with medium and large *Anapella* up the beach.

270681: *Anapella* groups I and III are positively correlated with *Wallucina* at lag 0. At small lags correlations between *Wallucina* and small and medium *Anapella* are bidirectional. At larger lags *Wallucina* tends to be correlated with medium *Anapella* up the beach.

290981: No correlations are significant at lag 0. Similar large-lag correlations occur as in the previous season but with a range of *Anapella* groups.

291281: As for 290981 but with consistent sign alternation with successive lags.

310382: Little correlation at any lag.

Soletellina

200381: Strong positive correlations exist between small *Anapella* and *Soletellina* at lag 0 . Correlations between small *Anapella* and *Soletellina* are typically positive at non-zero lags and there is little consistent bias in the direction of association.

270681: Soletellina is positively correlated with *Anapella* groups I and III at lag 0. At non-zero lags *Anapella* juveniles and *Soletellina* are correlated with little directional bias.

290981: Little significant correlations at any lags.

291281: Similar to 290981.

310382: No significant correlations at zero lag. At non-zero lags, associations are largely bidirectional and involve a range of *Anapella* groups.

Hydrococcus

200381: At lag 0 group II animals are positively correlated with medium and large *Hydrococcus* and negatively so (weak) with juvenile *Hydrococcus*. *Anapella* shows evidence of bidirectional relationships with *Hydrococcus* at non-zero lags. This is so for group II *Anapella* at small lags and the largest groups at large lags.

270681: Juvenile *Anapella* and group III *Hydrococcus* are positively correlated at zero lag. At other lags small *Hydrococcus* animals are often associated with medium *Anapella* up the beach while the correlations between small *Anapella* and most *Hydrococcus* are in the opposite direction. Larger *Anapella* and large *Hydrococcus* tend to have a bidirectional association. Lag 2 and 3 coefficients are mostly negative;

otherwise the terms are usually positive.

290981: At lag zero *Anapella* groups I and III are negatively correlated with *Hydrococcus* groups II and IV; large animals of each species are also negatively correlated. Overall, non-zero lag correlations are similar to the previous season but the sign changes are in the opposite direction.

291281: Juvenile *Hydrococcus* and medium *Anapella* are negatively associated at lag 0. Correlations are generally less significant than in previous seasons and there is less bidirectionality. Most associations are between small *Hydrococcus* and small *Anapella* up the beach.

310382: Juveniles of both species are positively correlated at lag 0 and small *Anapella* and medium *Hydrococcus* are negatively correlated at the same lag. At short and medium lags a range of *Anapella* groups are correlated with small *Hydrococcus* down the beach. At large lags a range of *Hydrococccus* groups are associated with medium *Anapella* up the beach.

Zeacumantus

200381: At lag 0 group II animals are positively correlated with small *Zeacumantus* . The strongest 200381 associations are found with *Zeacumantus* which is correlated with *Anapella* at all lags. The general pattern is for small and medium *Anapella* to be related to small *Zeacumantus* down the beach while *Zeacumantus* is often related to large *Anapella* up the beach. At short lags, these relationships are loosely bidirectional.

270681: Small *Anapella* are positively correlated with most *Zeacumantus* groups at lag 0 while larger *Anapella* and large *Zeacumantus* groups are negatively associated. Correlations at non-zero lags are generally bidirectional between a range of groups from each species.

290981: Positive associations occur between small *Anapella* and small and medium *Zeacumantus* and between large *Anapella* and medium *Zeacumantus* at lag 0. At other lags the correlations are as similar to those of the previous seasons.

291281: Medium *Anapella* are positively correlated with medium *Zeacumantus* at lag 0 while large animals of each species are negatively associated at that lag; otherewise, associations are as before.

310382: Strong positive associtaion occur between small/medium *Zeacumantus* and large *Anapella* and between large *Zeacumantus* and small *Anapella* at lag 0. Also at that lag, medium *Zeacumantus* is negatively correlated with medium *Anapella*. Correlations are again generally bidirectional at other lags.

Salinator

200381: At lag 0 group II *Anapella* associations are weakly negative with large *Salinator* while medium and large *Anapella* are often negatively correlated with *Salinator*. No consistent directional bias is evident at non-zero lags; only group I *Anapella* fails to show associations with *Salinator*.

270681: Total *Salinator* abundance is negatively correlated with group II *Anapella* at lag 0. Non-zero correlations are approximately as before.

290981: Both *Salinator* groups are negatively correlated with medium *Anapella* at lag zero; otherwise there is little apparent difference to previous seasons.

291281: At lag 0 group II *Anapella* and both *Salinator* groups are negatively correlated. At short and medium lags small *Anapella* are strongly correlated with *Salinator* abundances down the beach.

310382: Negative correlations occur between *Salinator* group I and *Anapella* group II and between *Salinator* group II and large *Anapella* at lag zero. There is a return to approximately bidirectional correlations at other lags.

Cylichnina

200381: No significant associations exist at lag zero. *Cylichnina* and small *Anapella* are associated at short lags in both directions.

270681: At lag 0 *Cylichnina* has strong positive associations with *Anapella* groups I and IV; it is negatively correlated with group V. At lag 1 *Cylichnina* is positively correlated with medium to large *Anapella* up the beach. Correlations are generally weak at larger lags.

290981: Juvenile *Anapella* and *Cylichnina* are positively correlated at lag 0. At short lags *Cylichnina* is negatively correlated with medium *Anapella* up the beach.

291281: No significant associations exist at lag zero. *Cylichnina* has positive correlations with juvenile and large *Anapella* at short lags. At larger lags these correlations are negative.

310382: Similar to the 200381 autumn.

Rissopsis

200381: Strong positive correlations exist between small *Anapella* and *Rissopsis* at lag 0. *Rissopsis* is typically correlated with the numbers of *Anapella* further up the beach. With increasing lag, the correlations occur with increasing sizes of *Anapella*. The sign of the coefficients alternates from positive (lag 0) through negative (lags 1, 2) to positive at lag 3 and negative at lag 4.

270681: *Rissopsis* and *Anapella* group III are positively associated at lag 0;

otherwise correlations are weak. Associations are typically with medium *Anapella*.

290981: *Rissopsis* and medium *Anapella* have a weak negative association at zero lag. Other lags are similar to 270681.

291281: At lag zero *Rissopsis* and large *Anapella* are negatively correlated. Correlations at other lags are generally bidirectional and involve medium *Anapella*.

310382: Large *Anapella* and *Rissopsis* have a strong positive correlation at lag 0. Associations between those animals continues at other lags and is generally bidirectional.

Microdiscula

200381: Medium and large *Anapella* are positively correlated with *Microdiscula* at lag 0. Correlations between large *Anapella* and *Microdiscula* at other lags are typically positive and there is little bias in the direction of association.

270681: No significant correlations occur at lag 0. At other lags correlations are typically bidirectional and involve medium and large *Anapella*.

290981: Group II *Anapella* and *Microdiscula* are positively associated at zero lag. Small and medium *Anapella* and *Microdiscula* have bidirectional correlations at non-zero lags.

291281: Similar to 290981 but no correlations are significant at lag 0.

310382: As for 291281 but the correlations involve large *Anapella* more frequently.

Nassarius

200381: *Nassarius* and medium *Anapella* are positively associated at lag 0. Correlations with medium and large *Anapella* also occur at short lags but no directional bias is evident.

270681: No lag 0 correlations are significant. At most non-zero lags bidirectional associations between *Nassarius* and medium and large *Anapella* are significant.

290981: As above.

291281: As above.

310382: *Nassarius* and large *Anapella* are positively associated at lag 0; otherwise as above.

Agatha

200381: Large *Anapella* are positively correlated with *Agatha* at lag 0. In general, *Agatha* is correlated with most *Anapella* groups in both directions.

270681: No correlations are significant at lag zero but otherwise the correlations are as above and most often involve medium and large *Anapella*.

290981: As above.

291281: As above.

310382: As above but group I and V *Anapella* are positively associated with *Agatha* at lag 0.

Bembicium

200381: Large *Anapella* are negatively correlated with *Bembicium* at lag 0. *Bembicium* and large *Anapella* are correlated in both directions at other lags.

270681: No significant correlations occur at lag zero. At non-zero lags most correlations involve small *Anapella* and are bidirectional.

290981: As above.

291281: As above.

310382: Group II *Anapella* and *Bembicium* are negatively associated at lag 0; otherwise as above.

Austrocochlea

200381: Medium *Anapella* are negatively, and large positively, correlated with *Austrocochlea* at lag 0. Commonly, *Austrocochlea* is associated with the number of large *Anapella* further up the beach while associations with medium *Anapella* are bidirectional.

270681: *Austrocochlea* and large *Anapella* are positively correlated at zero lag. Medium and large *Anapella* are often correlated with *Austrocochlea* down the beach.

290981: Correlations are generally weaker than in previous seasons. At lag 0 *Austrocochlea* is negatively associated with juvenile *Anapella* and positively associated with medium *Anapella*.

291281: Correlations are negligible at all lags.

310382: *Anapella* juveniles and *Austrocochlea* are negatively correlated at lag 0. Medium and large *Anapella* are often correlated with *Austrocochlea* down the beach.

Notoacmea

200381: No significant correlations occur at zero lag. At other lags *Notoacmea* and large *Anapella* have bidirectional associations.

270681: *Notoacmea* and group II *Anapella* are positively correlated at lag 0 (and negatively so at lag 1). *Notoacmea* is generally correlated with the number of medium and large *Anapella* up the beach.

290981: Group IV *Anapella* and *Notoacmea* have a positive association at zero lag and a bidirectional relationship otherwise.

291281: Correlations are relatively weak (none at lag 0) and involve medium *Anapella*.

310382: At lag 0 group II *Anapella* is positively correlated with *Notoacmea*. At long

lags *Notoacmea* is often correlated with medium *Anapella* up the beach; otherwise the relationships are bidirectional.

Anthopleura

200381: Medium *Anapella* are positively correlated with *Anthopleura* at lag 0. *Anthopleura* is generally correlated with large *Anapella* up the beach.

270681: At lag 0 group I and IV *Anapella* have negative correlations with *Anthopleura*. Little directional bias is evident.

290981: *Anthopleura* shows strong positive correlation with *Anapella* groups II, III and V at lag zero. Correlations at other lags usually involve medium *Anapella* and are bidirectional.

291281: Both *Anapella* group I and group V are positively related to *Anthopleura* at zero lag. Medium *Anapella* are often correlated with *Anthopleura* down the beach at non-zero lags.

310382: A positive correlation between large *Anapella* and *Anthopleura* is evident at lag 0; otherwise *Anthopleura* tends to be associated with medium and large *Anapella* up the beach.

Katelysia and

Wallucina

200381: There are no significant correlations at lag zero. At medium lags *Wallucina* and a number of *Katelysia* groups are bidirectionally correlated. Coefficient signs are positive at medium lags and negative at long lags.

270681: At lag 0 strong positive correlations exist with group II *Katelysia* and strong negative associations are evident with group V *Katelysia*. The sign of these correlations is the opposite at short lags; otherwise non-zero lag correlations are as before.

290981: *Wallucina* and group V *Katelysia* have a strong negative correlation at zero lag. These groups are positively related in both directions at short lags.

291281: Groups II and IV *Katelysia* are negatively associated with *Wallucina* at lag 0. The sign of these correlations is the opposite at short lags. Non-zero lag correlations are typically bidirectional and involve a variety of *Katelysia* groups.

310382: At lag 0 *Wallucina* and *Katelysia* and group IV are negatively correlated. Correlations at other lags are similar to those of previous seasons.

Soletellina

200381: No significant correlations occur at lag 0. At other lags *Soletellina* and large *Katelysia* tend to be correlated in both directions.

270681: *Katelysia* groups II and III have strong positive associations with *Soletellina*

at lag zero although the *Katelysia* total correlation is negative. Correlations at other lags involve most *Katelysia* groups and are bidirectional.

290981: *Katelysia* groups I, II and III are negatively, and groups IV and V positively, correlated with *Soletellina* at zero lag. Other lag correlations are similar to those of the previous season.

291281: At lag 0 *Soletellina* and *Katelysia* groups II and III are positively correlated. Other lag correlations are as before.

310382: Group III *Katelysia* is positively associated with *Soletellina* at zero lag. Other lag correlations are as before.

Hydrococcus

The between species correlations of the *Katelysia* and *Hydrococcus* distributions are stronger than for any other species pair in all seasons.

200381: At lag 0 *Katelysia* groups II and III are negatively correlated with *Hydrococcus* groups I and III and positively correlated with *Hydrococcus* group II; most *Katelysia* groups are positively associated with *Hydrococcus* group IV. At other lags the same groups consistently show bidirectional correlations with sign alternation between successive lags.

270681: Medium *Katelysia* are positively associated with all *Hydrococcus* at lag 0; similar correlations also exist between juvenile *Katelysia* and large *Hydrococcus*. At short lags small *Hydrococcus* are correlated with medium *Katelysia* up the beach. Other correlations are typically bidirectional and involve most groups of both species with sign alternation as before.

290981: All but the largest group of *Hydrococcus* are negatively correlated with medium and large *Katelysia* at lag 0. An exception is the association between juvenile *Hydrococcus* and group IV *Katelysia*, which is positive. At other lags most groups of *Hydrococcus* tend to be correlated with medium *Katelysia* up the beach.

291281: At lag 0 group II *Hydrococcus* is positively correlated with all *Katelysia* groups while *Hydrococcus* groups III and IV are negatively correlated with *Katelysia* groups I, II and IV. Non-zero lags are similar to those of the previous season.

310382: Juvenile *Hydrococcus* are positively, and other *Hydrococcus* negatively, correlated with group I and II *Katelysia* at lag zero. Other lag correlations are similar to those of previous seasons.

Zeacumantus

Correlations between *Katelysia* and *Zeacumantus* are negligible in all seasons.

Salinator

200381: At lag 0 *Salinator* group I is positively correlated with *Katelysia* groups I and IV. These groups are often correlated in both directions at other lags.

270681: *Katelysia* groups III and IV are negatively associated with group I *Salinator* at zero lag. At non-zero lags the principal correlations are bidirectional and involve group III *Katelysia* and group I *Salinator*.

290981: Overall correlations are strongest in this season. At lag 0 group I *Salinator* is positively correlated with group II *Katelysia* and negatively so with group V *Katelysia*. Both *Salinator* groups are involved in a number of bidirectional correlations with small and medium *Katelysia* at other lags.

291281: At lag zero group I *Salinator* and group I and II *Katelysia* are positively correlated, as are group II *Salinator* and group III *Katelysia*. At medium and large lags *Salinator* tends to be correlated with medium *Katelysia* up the beach.

310382: There are few significant correlations in this season.

Cylichnina

200381: No significant correlations occur at lag 0. At larger lags medium *Katelysia* tends to be associated with *Cylichnina* down the beach.

270681: Group I *Katelysia* and *Cylichnina* are positively associated at lag 0. Other lags are similar to 200381.

290981: Overall correlations are weaker in this season. At lag zero group I and II *Katelysia* are positively correlated with *Cylichnina*; other lag correlations tend to be bidirectional.

291281: *Cylichnina* and group IV *Katelysia* have a negative association at zero lag. Small and medium *Katelysia* are correlated with *Cylichnina* down the beach, particularly at short lags.

310382: At lag zero there is a negative correlation between group II *Katelysia* and *Cylichnina*. Other lags have correlations similar to those of previous seasons; in addition, *Cylichnina* is associated with medium *Katelysia* up the beach.

Rissopsis

200381: *Rissopsis* is positively correlated with large *Katelysia* at lag 0. These groups are generally correlated in both directions at other lags.

270681: At lag zero group I and II *Katelysia* are negatively associated with *Rissopsis*. Medium *Katelysia* and *Rissopsis* are generally correlated in both directions at other lags.

290981: Group III *Katelysia* is negatively, and group IV positively, correlated with

Rissopsis at lag zero. Other lag correlations are similar to those of the previous season.

291281: No significant correlations occur.

310382: No significant correlations occur.

Microdiscula

Correlations between *Katelysia* and *Microdiscula* are negligible in all seasons.

Nassarius

200381: Correlations are negligible apart from a weak association between *Nassarius* and large *Katelysia* at large lags.

270681: As above.

290981: As above.

291281: At lag zero *Nassarius* is positively correlated with *Katelysia* groups I, II, IV and V. Bidirectional correlations involving medium and large *Katelysia* occur at other lags.

310382: Group II *Katelysia* and *Nassarius* have a negative association at lag zero. At other lags small and medium *Katelysia* tend to be correlated with *Nassarius* down the beach.

Agatha

200381: *Agatha* is negatively correlated with *Katelysia* groups II and III, and postively correlated with *Katelysia* group IV, at zero lag. At other lags *Agatha* is generally correlated with small *Katelysia* up the beach; there is sign alternation between succesive lags.

270681: Correlations are minimal.

290981: As above.

291281: Apart from a positive correlation between *Agatha* and *Katelysia* groups I and II at lag 0, no significant correlations occur.

310382: Group I *Katelysia* and *Agatha* are positively associated at lag zero; otherwise correlations are negligible.

Bembicium

Correlations between *Katelysia* and *Bembicium* are negligible in all seasons.

Austrocochlea

200381: No significant correlations occur at lag 0. At other lags medium *Katelysia* and *Austrocochlea* are associated in both directions.

270681: *Austrocochlea* is positively correlated with medium and large *Katelysia* at lag zero. Correlations at other lags are relatively weak but otherwise are as in the previous season.

290981: At lag 0 group I, II and III *Katelysia* are negatively, and group IV positively, associated with *Austrocochlea*. Bidirectional correlations occur at other lags, mainly involving medium and large *Katelysia*.

291281: *Austrocochlea* is negatively correlated with *Katelysia* groups I, II and IV at zero lag. At other lags correlations are as above but most *Katelysia* groups are involved.

310382: At lag zero, small *Katelysia* are negatively correlated with *Austrocochlea*. Other correlations are generally as above.

Notoacmea

200381: Correlations are negligible.

270681: *Notoacmea* is positively correlated with group II and IV *Katelysia*. Correlations at other lags are loosely bidirectional and involve medium and large *Katelysia*.

290981: Group II *Katelysia* and *Notoacmea* are negatively correlated at zero lag. Other correlations are generally as above.

291281: A negative correlation exists between *Notoacmea* and group IV *Katelysia* at lag 0. Other correlations are generally as above.

310382: At lag zero *Notoacmea* is positively associated with large *Katelysia*. At other lags small *Katelysia* tend to be correlated with *Notoacmea* down the beach.

Anthopleura

200381: *Anthopleura* and large *Katelysia* are positively correlated at lag zero. At other lags correlations are generally bidirectional and involve both small and large *Katelysia*.

270681: At lag 0 group III *Katelysia* and *Anthopleura* are negatively associated. At non-zero lags medium and large *Katelysia* tend to be correlated with *Anthopleura* down the beach.

290981: *Anthopleura* and group I *Katelysia* are positively correlated at lag 0. Correlations at other lags are bidirectional and usually involve small *Katelysia*.

291281: *Anthopleura* and large *Katelysia* are positively correlated at lag zero. Correlations are relatively weak at non-zero lags and are usually with medium *Katelysia*.

310382: Correlations are negligible at all lags.

Wallucina and

Soletellina

200381: There are no significant correlations at lag 0 but at other lags *Wallucina* is correlated with *Soletellina* down the beach.

270681: The two species are positively associated at zero lag but other lags have little correlation.

290981: Correlations are negligible at all lags.

291281: *Wallucina* and *Soletellina* are negatively correlated at lag 0. At non-zero lags correlations exist but there is no obvious pattern.

310382: Correlations are negligible at all lags.

Hydrococcus

200381: Correlations are negligible.

270681: Correlations are negligible.

290981: Correlations are negligible.

291281: At lag 0 *Wallucina* is positively correlated with group III and IV *Hydrococcus*. At other lags medium and large *Hydrococcus* tend to be correlated with *Wallucina* down the beach.

310382: No significant associations occur at zero lag but at other lags the correlations are similar to those of the previous season.

Zeacumantus

Correlations between *Wallucina* and *Zeacumantus* are minimal in all seasons.

Salinator

As above.

Cylichnina

As above.

Rissopsis

As above.

Microdiscula

As above.

Nassarius

Correlations between *Wallucina* and *Nassarius* are minimal in most seasons; in the 310382 autumn there is a weak bidirectional relationship.

Agatha

Correlations between *Wallucina* and *Agatha* are negligible in all seasons.

Bembicium

Correlations between *Wallucina* and *Bembicium* are minimal in all seasons.

Austrocochlea

200381: Correlations are negligible.

270681: Correlations are negligible.

290981: Correlations are negligible.

291281: At lag 0 *Wallucina* and *Austrocochlea* are positively correlated. Other lags have weak correlations.

310382: *Wallucina* and *Austrocochlea* have a negative association at zero lag and a bidirectional relationship at short lags.

Notoacmea

200381: Correlations are negligible.

270681: Although no significant correlations exist at lag 0, at other lags the two species tend to have a bidirectional relationship.

290981: Correlations are negligible.

291281: *Wallucina* and *Notoacmea* are positively correlated at zero lag. Correlations are weak at other lags.

310382: *Wallucina* and *Notoacmea* are negatively correlated at zero lag. At short lags the two species have a bidirectional relationship.

Anthopleura

200381: At lag 0 *Wallucina* and *Anthopleura* are negatively correlated. Strong bidirectional correlations are evident at other lags.

270681: Correlations are weak.

290981: Correlations are weak.

291281: Correlations are weak.

310382: Correlations are negligible.

Soletellina and

Hydrococcus

200381: Group IV *Hydrococcus* is positively correlated with *Soletellina* at lag zero. At shost lags small and large *Hydrococcus* are associated with *Soletellina* up the beach. There is an alternation of sign with successive lags.

270681: Although no correlations are significant at lag 0 group III and IV *Hydrococcus* are correlated with *Soletellina* up the beach.

290981: *Soletellina* and group II *Hydrococcus* are positively correlated at lag zero. At other lags the two species are loosely correlated in both directions.

291281: At lag 0 juvenile *Hydrococcus* and *Soletellina* are positively associated. Most correlations at other lags involves medium and large *Hydrococcus* which are

correlated with *Soletellina* up the beach.

310382: *Soletellina* is negatively correlated with *Hydrococcus* groups II, III and IV at lag zero. Other lag correlations are as above.

Zeacumantus

Correlations between *Soletellina* and *Zeacumantus* are negligible in all seasons.

Salinator

200381: At lag 0 *Soletellina* and group I *Salinator* are negatively correlated. At other lags those groups are weakly associated with little directional bias.

270681: Group II *Salinator* and *Soletellina* are negatively correlated at zero lag. *Salinator* tends to be correlated with *Soletellina* down the beach at other lags.

290981: Similar to above but no correlations at lag 0.

291281: Correlations are generally weak and have little directional bias.

310382: Correlations are weak although at large lags *Salinator* is associated with *Soletellina* up the beach.

Cylichnina

200381: Correlations are generally weak and have little directional bias.

270681: Correlations are negligible.

290981: At lag zero *Soletellina* and *Cylichnina* are positively correlated. Significant correlations betwen the two species exist at other lags but there is no definite directional bias.

291281: Correlations are weak.

310382: Correlations are negligible.

Rissopsis

200381: Correlations are weak.

270681: At lag 0 the two species are negatively correlated. At other lags there is a definite bidirectional correlation with alternating sign, particularly at short lags.

290981: As above but non-zero lag correlations are less defined.

291281: Correlations are negligible.

290981: Correlations are negligible.

Microdiscula

Correlations between *Soletellina* and *Microdiscula* are negligible in all seasons.

Nassarius

Correlations between *Soletellina* and *Nassarius* are negligible in all seasons.

Agatha

Correlations between *Soletellina* and *Agatha* are negligible in all seasons.

Bembicium

Correlations between *Soletellina* and *Bembicium* are negligible in all seasons.

Austrocochlea

200381: Correlations are negligible.

270681: Correlations are negligible.

290981: A strong negative correlations exists between the two species at lag zero. At non-zero lags *Austrocochlea* tends to be associated with *Soletellina* up the beach.

291281: No significant correlations exist at lag zero and correlations at other lags are weak with no directional bias.

310382: Correlations are negligible.

Notoacmea

200381: Correlations are negligible.

270681: No significant correlations exist at lag zero and at other lags Notoacmea is correlated with *Soletellina* up the beach.

290981: The two species are negatively correlated at lag 0. At other lags the correlations are bidirectional.

291281: Correlations are weak.

310382: At lag 0 *Soletellina* and *Notoacmea* are positively associated; other lags have bidirectional relationships.

Anthopleura

Correlations between *Soletellina* and *Anthopleura* are weak in all seasons.

Hydrococcus and

Zeacumantus

200381: At lag 0 group II *Hydrococcus* is positively correlated with group I *Zeacumantus* while at short lags it is bidirectionally associated with group III *Zeacumantus* .

270681: Group II and III Hydrococcus are positively correlated with group III *Zeacumantus* at lag zero. At larger lags *Zeacumantus* is generally associated with large *Hydrococcus* up the beach. There is evidence of sign alternation with successive lags.

290981: At lag 0 negative correlations occur between group I *Zeacumantus* and group III *Hydrococcus* and between group II *Zeacumantus* and group II and IV *Hydrococcus* . At other lags correlations between the two species are loosely bidirectional.

291281: At lag zero group I *Zeacumantus* is negatively correlated with group I and II *Hydrococcus* while group I *Hydrococcus* and group III *Zeacumantus* are positively

correlated. At larger lags small *Zeacumantus* are associated with *Hydrococcus* up the beach although the directional bias is weak.

310382: Group I of each species are negatively associated at lag 0. At larger lags group I *Zeacumantus* is associated with group I *Hydrococcus* up the beach while group II *Hydrococcus* is correlated with small *Zeacumantus* down the beach.

Salinator

200381: Group I *Salinator* and group III *Hydrococcus* are positively associated at zero lag. Correlations between the two species at other lags involve a range of groups and show no evidience of directional bias.

270681: At lag 0 group I *Salinator* is negatively correlated with *Hydrococcus* groups I, II and III; group II *Salinator* is positively correlated with group IV *Hydrococcus*. Non-zero lag correlations are generally bidirectional, particularly between group I of each species at short lags. At larger lags, however, *Salinator* tends to be associated with *Hydrococcus* up the beach.

290981: A positive correlation between group II *Salinator* and group I *Hydrococcus* exists at lag 0. At lag 1 *Salinator* is correlated with small *Hydrococcus* up the beach; otherwise non-zero lags typically show correlations between *Hydrococcus* and *Salinator* down the beach.

291281: Groups I and II of *Hydrococcus* and *Salinator* are positively correlated at lag 0. Generally small *Salinator* is associated with *Hydrococcus* up the beach at other lags.

310382: At lag zero positive correlations between group I of *Salinator* and *Hydrococcus* and between group II *Salinator* and *Hydrococcus* groups I and II. Directional bias at other lags is poorly defined but *Salinator* does tend to be correlated with small *Hydrococcus* up the beach.

Cylichnina

200381: Correlations are weak, particularly at short lags.

270681: As above.

290981: As above.

291281: At lag 0 *Cylichnina* is positively correlated with *Hydrococcus* groups III and IV. At other lags small and medium *Hydrococcus* are bidirectionally correlated with *Cylichnina*.

310382: Correlations are weak, particularly at short lags.

Rissopsis

200381: Correlations are weak, particularly at short lags.

270681: *Rissopsis* is negatively correlated with group III *Hydrococcus* at lag zero. No directional bias is evident at other lags.

290981: At lag 0 *Rissopsis* is positively associated with group I and IV *Hydrococcus*. At short lags *Rissopsis* is correlated with *Hydrococcus* up the beach; otherwise there is little directional bias.

291281: Correlations are weak, particularly at short lags.

310382: Correlations are weak, particularly at short lags.

Microdiscula

200381: Correlations are weak.

270681: As above

290981: Although there are no significant correlations at lag 0, the two species are correlated in both directions at other lags.

291281: Correlations are weak.

310382: As above.

Nassarius

200381: Correlations are weak.

270681: As above.

290981: *Nassarius* is positively correlated with all *Hydrococcus* groups at lag zero. There is no consistent directional bias at other lags.

291281: At lag 0 *Nassarius* is negatively associated with group I and III *Hydrococcus*. Other lags are as above.

310382: *Hydrococcus* groups III and IV are positively correlated with *Nassarius* at lag 0. Other lags are as above.

Agatha

200381: *Agatha* is positively correlated with *Hydrococcus* groups I and II, and negatively correlated with group III, at lag 0. At non-zero lags the two species are generally correlated in both directions.

270681: Correlations are weak.

290981: There are no significant correlations at lag 0; at other lags *Agatha* is loosely associated with *Hydrococcus* up the beach.

291281: Associations are generally weak although group I *Hydrococcus* and *Agatha* are negatively correlated at lag 0.

310382: Correlations are weak at short lags and there is little directional bias.

Bembicium

200381: Correlations are weak.

270681: Correlations are weak at short lags; at larger lags *Bembicium* is correlated with large *Hydrococcus* up the beach.

290981: Correlations are weak at short lags; at larger lags *Hydrococcus* is loosely associated with *Bembicium* down the beach.

291281: *Bembicium* is positively correlated with group I and II *Hydrococcus* at lag zero. Associations have little directional bias at short lags and are negligible at larger lags.

310382: *Bembicium* is positively correlated with group I and II *Hydrococcus* at lag 0 but associations are negligible at other lags.

Austrocochlea

200381: Correlations are negligible at lag 0. At other lags the two species have a bidirectional relationship.

270681: Correlations are weak.

290981: Juvenile *Hydrococcus* are positively associated with *Austrocochlea* at lag 0. There is no evidence of a directional relationship at non-zero lags.

291281: Group III and IV *Hydrococcus* are positively correlated with *Austrocochlea* at zero lag. Otherwise associations are as above.

310382: At lag 0 *Austrocochlea* has a negative associations with group I *Hydrococcus* and a positive correlation with other groups. Non-zero lag correlations are generally weak.

Notoacmea

200381: Correlations are weak at short lags and generally bidirectional with *Hydrococcus* group II at longer lags.

270681: Correlations are weak.

290981: Group I and IV *Hydrococcus* are negatively associated with *Notoacmea* at lag zero. Correlations at non-zero lags are bidirectional and usually involve medium *Hydrococcus* .

291281: No significant correlations occur at lag 0; otherwise *Hydrococcus* tends to be correlated with *Notoacmea* down the beach.

310382: As above.

Anthopleura

200381: A weak positive association between group IV *Hydrococcus* and *Anthopleura* at zero lag. At longer lags *Hydrococcus* tends to be associated with *Anthopleura* down the beach.

270681: Correlations are weak.

290981: As above.

291281: As above.

310382: As above.

Zeacumantus and

Salinator

200381: At lag zero group II *Salinator* is negatively correlated with *Zeacumantus* groups II and III. There is no consistent directional bias at non-zero lags.

270681: Correlations are weak.

290981: As above.

291281: Group I *Zeacumantus* is negatively correlated with both *Salinator* groups, and group III positively with group I *Salinator*, at lag 0. Correlations at other lags are generally bidirectional.

310382: At zero lag *Salinator* group I is negatively associated with *Zeacumantus* groups I and II; otherwise correlations are as above.

Cylichnina

200381: Correlations are negligible.

270681: At lag 0 *Cylichnina* is positively correlated with total *Zeacumantus* and all *Zeacumantus* groups are negatively associated with *Cylichnina* down the beach at lag 1. Otherwise, correlations are negligible.

290981: *Cylichnina* and medium and large *Zeacumantus* are bidirectionally associated at medium lags; at zero and long lags correlations are negligible.

291281: Correlations are negligible.

310382: Correlations are negligible.

Rissopsis

200381: Correlations are negligible.

270681: As above.

290981: As above.

291281: *Rissopsis* is positively correlated with medium *Zeacumantus* at lag 0. At non-zero lags medium and large *Zeacumantus* are associated with *Rissopsis* down the beach.

310382: At lag 0 all *Zeacumantus* groups are positively correlated with *Rissopsis*. The two species are associated in both directions at other lags.

Microdiscula

200381: Correlations are negligible except for a bidirectional relationship at medium lags.

270681: No significant correlations occur at lag 0. At short lags *Microdiscula* is associated with medium and large *Zeacumantus* up the beach.

290981: *Microdiscula* and *Zeacumantus* groups I and II are positively correlated at lag 0. At short lags *Microdiscula* is associated with large *Zeacumantus* up the beach.

291281: No significant correlations occur at lag 0. At short lags *Microdiscula* is associated with group I *Zeacumantus* up the beach and medium/large *Zeacumantus* are correlated with *Microdiscula* down the beach.

310382: *Microdiscula* and medium *Zeacumantus* are negatively associated at lag zero. At other lags *Microdiscula* is correlated with *Zeacumantus* up the beach.

Nassarius

200381: No significant correlations occur at lag 0. *Nassarius* is bidirectionally associated with small and medium *Zeacumantus* at non-zero lags.

270681: At lag 0 all *Zeacumantus* groups are positively correlated with *Nassarius*. The two species are bidirectionally associated at other lags.

290981: Group I *Zeacumantus* and *Nassarius* are negatively correlated at lag zero. Other lags are as above.

291281: Correlations are weak.

310382: Similar to the 200381 autumn.

Agatha

200381: Medium *Zeacumantus* and *Agatha* are negatively correlated at lag 0. At other lags *Agatha* and small/medium *Zeacumantus* are bidirectionally associated.

270681: At lag 0 group I *Zeacumantus* is negatively correlated with *Agatha*. Correlations at other lags have no directional bias and are relatively weak.

290981: Medium *Zeacumantus* and *Agatha* are positively correlated at lag 0. Bidirectional correlations between the two species exist at other lags.

291281: At lag 0 *Agatha* is negatively correlated with small and medium *Zeacumantus*. Other lags are as above.

310382: Small *Zeacumantus* and *Agatha* are positively correlated at zero lag. Other lags are generally as above.

Bembicium

200381: Group II and III *Zeacumantus* are positively correlated with *Bembicium* at lag zero. Bidirectional correlations between the two species exist at other lags.

270681: Correlations are weak at short lags and have no well defined directional bias at other lags.

290981: Correlations are relatively weak and have no directional bias.

291281: At lag zero *Bembicium* is negatively correlated with small, and positively with medium and large, *Zeacumantus* . No well defined directional bias exists at other lags.

310382: Small *Zeacumantus* and *Bembicium* are negatively associated at lag 0; otherwise, lags generally show *Zeacumantus* correlated with *Bembicium* down the beach.

Austrocochlea

200381: No significant correlations occur at lag 0 but at other lags *Austrocochlea* is bidirectionally associated with small *Zeacumantus* .

270681: As above but correlations involve the range of *Zeacumantus* groups.

290981: Correlations are generally weak although small *Zeacumantus* is negatively correlated with *Austrocochlea* at lag zero.

291281: Correlations are negligible.

310382: Correlations are weak.

Notoacmea

Correlations between *Zeacumantus* and *Notoacmea* are negligible in all seasons.

Anthopleura

200381: Correlations are weak.

270681: Correlations are negligible.

290981: Correlations are negligible.

291281: At lag 0 group II and III *Zeacumantus* are negatively correlated with *Anthopleura* . At other lags these groups are associated in both directions.

310382: No significant correlations occur at lag zero. At non-zero lags *Anthopleura* tends to be associated with *Zeacumantus* up the beach.

Salinator and

Cylichnina

200381: Correlations are weak.

270681: Correlations are negligible apart from a positive correlation between the two species at lag 0.

290981: Correlations are weak.

291281: At lag 0 *Cylichnina* is positively correlated with total *Salinator*. Bidirectional associations occur at medium lags but correlations are otherwise negligible.

310382: Correlations are negligible.

Rissopsis

200381: Correlations are weak.

270681: *Rissopsis* is positively correlated with both groups of *Salinator* at lag zero.

290981: *Rissopsis* is positively correlated with group II *Salinator* at lag zero. Other lag correlations are generally bidirectional.

291281: Correlations are weak.

310382: As above.

Microdiscula

Correlations between *Salinator* and *Microdiscula* are weak in all seasons.

Nassarius

As above.

Agatha

As above.

Bembicium

200381: Correlations are weak.

270681: *Salinator* group II is positively correlated with *Bembicium* at zero lag. There is no consistent directional bias at non-zero lags.

290981: As above.

291281: As above except that the lag 0 correlations involve both *Salinator* groups.

310382: As above.

Austrocochlea

200381: Correlations are weak.

270681: As above.

290981: At lag 0 *Austrocochlea* is negatively correlated with both *Salinator* groups. At non-zero lags correlations are approximately bidirectional.

291281: Correlations are weak.

310382: As above.

Notoacmea

200381: Correlations are weak.

270681: *Notoacmea* and group II *Salinator* are negatively correlated at lag 0. At short lags *Salinator* is associated with *Notoacmea* down the beach.

290981: Both *Salinator* groups are negatively correlated with *Notoacmea* at lag zero. Little directional bias is evident at non-zero lags.

291281: Correlations are relatively weak although *Notoacmea* is positively correlated with both *Salinator* groups at lag 0.

310382: Correlations are negligible.

Anthopleura

Correlations between *Salinator* and *Anthopleura* are negligible in all seasons.

Correlations between the remaining species (*Cylichnina*, *Rissopsis*, *Microdiscula*, *Nassarius*, *Agatha*, *Bembicium*, *Austrocochlea*, *Notoacmea* and *Anthopleura*) are inconsistent in all seasons.

5.4 Discussion

5.4.1 Serial correlation with physical factors

Exposure appears to be an important, but not overiding, factor in determining the distribution and abundance of organisms on the tidal flat. The distributions of the most abundant bivalve, *Anapella*, and the most abundant gastropod, *Hydrococcus*, are largely independent of beach height. In contrast, the other common bivalve, *Katelysia*, shows strong positive correlations with depth below EHWS throughout the year, particularly the smaller animals. The second most abundant gastropod, *Zeacumantus*, also shows a restricted zonation, but in the upper half of the beach.

Katelysia scalarina appears to show a general preference for low tidal zonation (Guiler 1950; Wells and Threlfall 1980; Wells and Roberts 1980), suggesting a lack of tolerance to dessication. An alternative explanation could be that *Katelysia* is a stronger competitor for space than *Anapella*, and is thus able to exclude that species from low areas of the beach (which provide longer feeding times). However the strongest correlations with depth would then be expected among large *Katelysia*; this is not the case.

Hydrococcus is distributed over most of the beach but numbers tend to increase with beach depth. In Western Australia, however, *Hydrococcus* (*graniformis*) *brazieri* numbers reach a peak near the middle of the tidal flats of Oyster Harbour and Peel Inlet (Wells and Threlfall 1980). Similarly, the distributions of related hydrobid species in Europe are correlated more strongly with sediment types and salinities than with exposure (Fenchel 1975; Fenchel and Kofoed 1976), although Wells (1978) found depth to be one of the principal determinants of the distribution of *Hydrobia* in Nova Scotia. It the present study, *Hydrococcus* individuals were often found up to 10 cm above the substrate, on the marker stakes; this occurred at most stations. It is likely, therefore, that the positive correlations between *Hydrococcus* abundance and depth are reflections of underlying causes, rather than tolerance to exposure.

The other deposit feeding gastropod, *Salinator*, shows variable correlations with depth, both in terms of the strength and the sign of the associations. *Salinator* is tolerant of exposure for long periods and is frequently found in the high intertidal (Smith and Kershaw 1979). Its distribution appears to be relatively independent of beach height (Wells and Roberts 1980; Wells and Threlfall 1980). In Pipe Clay Lagoon, small *Salinator* are positively correlated with depth in winter and spring but in those seasons the animals are uncommon. The negative correlations shown at other times of the year are opposite to those of *Hydrococcus*, a possible competitor.

The only other species exhibiting significant (negative) correlations between abundance and depth is *Bembicium* , which forms a very narrow zone at the extreme top of the beach.

A number of the lagoon species show correlations between abundance and sediment grain size. The size fractions of the sediments can be conveniently divided into fine (< 125 µm) and medium (> 125 µm) types (after Gray 1981), according to the faunal associations; these tend to be of opposite sign for each type. The medium type comprises the bulk (80-90%) of the sediment. *Katelysia* , *Hydrococcus* and *Salinator* show negative correlations with fine sands, as do *Cylichnina* and small *Anapella*. The correlations shown by *Cylichnina* are probably due to an underlying correlation with the distribution of *Hydrococcus* juveniles. *Microdiscula* and *Zeacumantus* are positively correlated with the same sediment type. Only in autumn do these correlations extend to sediments less than 63 µm in diameter. The majority of the above associations are of opposite sign for the medium size sands.

Grange (1977) found that deposit feeders were most abundant in 'fine' sands while suspension feeders preferred 'medium' sands. He suggested that the optimum grain size for deposit feeders was 2.6 phi units (c. 160 µm) and the optimum grain size for suspension feeders was 1.9 phi units (c. 260 µm). Both these optimum values lie in the medium size sediment type of the present study; it is not possible to be more specific about the preferred sediment sizes of the Pipe Clay Lagoon species.

The apparent preference for the medium sands over fine sands shown by the deposit feeders may be a reflection of a selection of more predictable sediment types (the size fraction less than 63 µm is particularly variable in its distribution). In such well sorted sediments, species dependent on relatively uncommon grain sizes would be disadvantaged. The larger sediment particles could also be more likely to have organic encrustations (Hughes 1979; Whitlach 1980).

Zeacumantus shows a clear preference for sediment grains smaller than those selected by the deposit and suspension feeders. This may be evidence of resource partitioning between different trophic groups. By feeding on encrusting algae on fine sands, or microalgae and foraminiferans in the interstitial spaces of fine sands, *Zeacumantus* could avoid interference competition from the deposit feeders. The differences in particle size selection are not sufficient to lead to spatial segregation between *Zeacumantus* and the deposit feeders, however. Again, this could be due the high sediment sorting throughout the beach. Segregation might occur on a scale of millimeters rather than meters.

Microdiscula probably feeds in a manner similar to other Skeneopsidae, rasping algae and diatoms off solid surfaces (Chapter 2). Large (relative to the body size of *Microdiscula*) sediment grains would provide a more stable rasping surface than small grains. It is therefore surprising that *Microdiscula* is positively correlated with fine sediments. *Microdiscula* might be dependent on a food resource only found on fine sands, and similar to that used by *Zeacumantus* . Indeed, both species show similar distributions over the transects (Chapter 4).

Shell debris would also provide a solid surface for microalgae encrustations but the rasping species (*Microdiscula* and *Notoacmea*) do not appear to take advantage of this. The debris would be relatively mobile and appears to be deposited against beach slopes. The correlations shown by *Anapella* , *Zeacumantus* and *Salinator* are likely to be a reflection of this, and not indications of causal relationships.

Correlations between species distributions and the organic content of sediments are difficult to interpret because of their interdependence. While deposit feeders often reach their highest densities in organic-rich substrates (Whitlach 1980), those animals are capable of eventually reducing the organic content (Tsuchiya and Kurihara 1980). Each case would lead to correlations of opposite sign. Also, while the abundance of suspension feeders is usually independent of the substrate's organic content, an abundance of fine, particulate organic matter may interfere with the suspension feeding structures (Rhoads and Young 1970), thus producing negative correlations similar to those exhibited by *Anapella* and *Katelysia* .

In Pipe Clay Lagoon, *Salinator* reaches its highest abundance on the upper shore slope and shows a strong positive correlation with the organic content of those sediments. It appears that *Salinator* is unable to reduce the organic loading of the substrate. In contrast, *Hydrococcus* shows negative associations with organic content, suggesting that high animals densities lead to a depletion of the organic material resources.

The *Anapella* , *Katelysia* and *Hydrococcus* correlations could be partly due to their underlying correlations with fine sand grains. Particulate organic matter is usually correlated with the distribution of fine sediment particles (Pugh *et al* 1974; Tietjen 1977; Tsuchiya and Kurihara 1980) and it is difficulte to separate relationships involving one or the other.

The associations between the species distributions and the distributions of the polychaete worm tubes can be separated according to the trophic groups. The suspension feeding bivalves, *Anapella* and (large) *Katelysia* , are generally positively correlated with the worm tubes while the deposit feeding gastropods, *Hydrococcus* and *Salinator* ,

and also *Zeacumantus* , frequently show negative correlations. These associations are probably related to the actions of the worm tubes in stabilising the substrate. Suspension feeders are commonly associated with stable substrates which provide a secure anchorage and which prevent the clogging of feeding structures (Jackson 1972; Eagle 1973; Biernbaum 1979; James and Gibson 1980; Brown 1982; Gallagher *et al* 1983).

Deposit feeding would be restricted in sediments bound together by worm tubes. Conversely, bioturbation by deposit feeders might prevent the establishment of tube building, suspension feeding polychaetes. Both these factors could account for the negative correlations between the abundances of worm tubes and the abundances of *Hydrococcus* , *Salinator* and *Zeacumantus* . It is possible that the relationship between the deposit feeders and the polychaetes involves a negative feedback mechanism.

Like the shell debris, the algal mats would be relatively mobile and subject to distribution by water currents. Most correlations with species distributions, therefore, are probably not causal relationships. However, the positive association shown by *Rissopsis* may be a genuine relationship. Rissoids are often trapped by macroalgae and this appears to be a major factor determining the distribution of those species (Wigham 1975).

5.4.2 Serial autocorrelation

It is clear that the distributions and abundances of many species are influenced by physical characteristics of the beach. A number of species also show evidence of autocorrelations along the distribution transects, suggesting that the abundance of a given species at at given position on the transect is partly determined by the abundance of that species some distance along the transect.

Many of the autocorrelograms show an alternation of signs with successive lags. This suggests that the range of the autocorrelations extends no more than 20 m along the beach. In these cases, significant correlations at lags greater than 20 m are probably anomalies due to the mathematical shifting of two fluctuating series with respect to each other. If one series is oscillating about another with a frequency of approximately half the sampling frequency, that curve will alternately appear higher and lower than the reference curve. In terms of the species distributions, this corresponds to a correlation between two series (or one series shifted relative to itself) operating over a lag of one sampling distance.

Few of the serial correlations show a consistent sign over a range of successive lags. This makes it difficult to infer the true sign of the correlations. If, for example, a serial correlation was operating over a distance of only a few metres (rather than $\geq$ 20 m)

the 20 m sampling intervals would be too coarse. The interpretation of the correlograms is fraught with scale problems similar to those associated with the choice of quadrat size. However, while it is difficult to determine the sign and scale of the correlations at non-zero lags, the correlograms do at least allow the existence of serial correlations to be ascertained. If there are also significant correlations at lag zero, then similar coefficient signs at non-zero lags can be inferred.

A number of *Katelysia* size classes and size groups are significantly autocorrelated. The correlations are typically negative at a lag of 20 m, with the sign of the correlation coefficients alternating with successive lags. *Katelysia* autocorrelations are strongest in spring and summer when they occur in a range of size classes. In autumn, autocorrelations are mainly restricted to juvenile animals. In winter, autocorrelations are evident in adult animals. This is the peak breeding season and suggests that breeding adults interact along the tidal gradient. In spring and summer, similar interactions extend to young animals.

Hydrococcus autocorrelations are uncommon and are largely confined to the smallest size class. In the 200381 autumn negative correlations extend over at least 60 m, suggesting a strong spatial separation of juvenile *Hydrococcus* along the beach profile. This is one of the few cases when the sign of the correlation can be determined with any certainty. By winter, the scale of the negative correlation reduces to the order of 20 m. Autocorrelations do not occur in the peak breeding season (spring).

Other species that show significant serial autocorrelations (*Wallucina*, *Soletellina*, *Cylichnina*, *Rissopsis*, *Nassarius* and *Austrocochlea*) frequently have correlograms similar to those of *Katelysia* adults in winter. This suggests that those patterns are an artifact of the statistical analysis and not true indications of serial relationships. The artifact appears to arise most often in uncommon species and limits the usefulness of series analysis for examining the autocorrelations of those species. Unfortunately, it also throws doubt on the validity of the winter correlograms of *Katelysia*.

There appear to be no other studies of serial autocorrelation of species abundances along an environmental gradient; the present study suggests that the technique has limited value. This could be largely due to a lack of fidelity in the sampling process, and future studies might benefit from a more detailed sampling program. Unfortunately, however, the time and effort required for such intensive sampling could become prohibitive.

5.4.3 Serial intraspecific cross-correlation

The serial cross-correlation analysis provides more useful information than the autocorrelation analysis. The cross-correlograms show consistent relationships between a number of species groups and also between a number of species. The major difficulty in interpreting the correlograms lies in placing a value on the inconsistent relationships. The interpretor must address the question: 'Is a singly occurring correlation less meaningful than one that occurs consistently?' Perhaps the best approach is that which is often useful in ecological studies - "squinting". If the examination of the correlograms is "blurred", the strongest, most consistent patterns will be emphasised.

The analysis, therefore, represents a hierarchical reduction in the information content of the community. The initial sampling procedure produces a data subset of the natural community; this, in turn, is condensed by identifying non-zero correlations within the data subset. Those correlations are further reduced by contructing a correlogram using only the correlations that achieve a required level of significance. Finally, the correlograms are examined for the strongest and most consistent relationships. An unavoidable problem arising from this approach is the introduction of subjectivity into the analysis.

This subjectivity, however, does not necessarily detract from the usefulness of the analytical methods. It is analogous to the natural history approach of the early biologists, common when that discipline was in its infancy. Advances in our understanding of the natural world proceeded only through the observation and cataloguing of the behaviour of individual species. Similarly, with community ecology in a stage of relative infancy, the best approach involves the observation and cataloguing of the behaviour of species complexes. The (objective) statistical analysis is necessary to reduce the enormous complexity of the community to manageable proportions.

In Pipe Clay Lagoon, serial cross-correlations between conspecific groups appear to generally reflect the breeding patterns of the species. The bivalves, *Anapella* and *Katelysia*, have a planktonic larval stage and the serial correlations suggest that spatfall at a given position on the beach is often dependent on the number of adults some distance further down the beach. In contrast, the gastropods, *Hydrococcus* and *Zeacumantus*, typically show bidirectional correlations that operate over shorter distances.

Winter is the season of least serial interaction between *Anapella* groups. Also, in that season, the distribution of juveniles is correlated with the number of adults further up the beach. Both these factors are likely to be result from *Anapella* reproduction extending over most of the tidal flat - breeding by adults high on the winter beach leads to

spatfall on lower areas of the beach. This indicates that the wave of recruitment success passing up the beach over the cooler months is at least partly due to a corresponding wave of reproduction effort, and not simply a change in spat survival. In summer spatfall is primarily due to adults breeding in the lower areas of the beach. These patterns may be influenced by other factors, such as migration, that were not examined.

Katelysia shows considerably more interactions between its groups than does *Anapella* (as was the case for the autocorrelations). The correlations suggest that the peak spring spatfall of *Katelysia* is due mainly to adults breeding lower on the beach. *Katelysia* spatfall is never dependent on breeding adults higher on the beach.

Hydrococcus interactions are generally bidirectional and weaken considerably with increasing lag. This is probably due to the absence of a planktonic larval stage. The distribution of *Hydrococcus* ~~spat~~ larvae appears to be relatively independent of dispersal by water currents. In autumn, juvenile *Hydrococcus* are negatively correlated with other *Hydrococcus* groups, suggesting a spatial segregation along the transect.

Zeacumantus also shows evidence of spatial segregation, but this occurs in summer. Like *Hydrococcus* , *Zeacumantus* interactions are generally independent of direction along the transect. In winter both *Hydrococcus* and *Zeacumantus* show correlations between large animals and small animals further up the beach (the reverse correlations are not significant); the number of juveniles high on the beach influences the distribution of large animals lower on the beach.

The serial cross-correlation analysis has revealed juvenile-adult dependences that can largely be attributed to the reproductive patterns of each species, and that can explain many of the changes in the population structures of the species along the beach profile. The principal determining factors of the bivalve population structures appear to be a combination of season, position of adults on the beach and dispersal of the planktonic larvae. These factors have frequently been implicated as factors controlling the distribution of species having a planktonic larval phase (Matthiessen 1960; Dakin 1966; Brown 1982; Gianuca 1983). Larval dispersal, in particular, can account for differences in the distributions of adults and juveniles. Migration and passive resettlement may also be important, but were not examined.

In contrast, the different size groups of the gastropods have similar distributions over most of the beach and the juvenile-adult dependences are not greatly affected by dispersal. Also, the dependences are not only related to reproduction. Both *Hydrococcus* and *Zeacumantus* adults show a degree of dependence on the abundance of juveniles. The interactions appear sufficiently intense to influence the distribution of the different size classes along the transect.

5.4.4 Serial interspecific cross-correlation

The between-species cross-correlation analysis has also highlighted numerous interactions. These are best considered according to the suggested functional groups of the species, beginning with the major suspension feeders.

The series analysis reveals evidence of spatial segregation between *Anapella* and *Katelysia* only in one season and only between juveniles - lag zero correlations are generally positive, except between juveniles in autumn. This suggests that the segregation between similarly sized animals, illustrated in Chapter 4, is not actively maintained. The segregation may, however, be a historical segregation, resulting from adaptations by one or both species. Alternatively, the grouping of size classes prior to the series analysis may have prevented the detection of subtle associations between individual size classes.

The positive lag zero correlations frequently involve the smaller groups. Correlations at non-zero lags, however, are between groups of markedly different sizes. Usually small *Anapella* are correlated with larger *Katelysia*. In winter, similar associations occur between small *Katelysia* and larger *Anapella*. In all seasons, *Anapella* is correlated with *Katelysia* down the beach and *Katelysia* is correlated with *Anapella* up the beach. This suggests that large *Katelysia* may exclude juvenile *Anapella* from the lower parts of the beach; similarly, large *Anapella* may exclude juvenile *Katelysia* from the upper sections of the beach. These exclusions are most apparent in the seasons of major recruitment. Note that 'exclusions' do not necessarily lead to negative cross-correlations at non-zero lags. The community is far from a simplistic ideal and the important feature of the associations at non-zero lags is their significance, rather than their sign. Cross-correlations at much smaller spacings are considered in the next chapter and will provide a stronger test of the associations.

Wallucina and *Soletellina* show strong serial correlations with *Anapella* only in the 200381 autumn and the winter. These relationships are positive although *Wallucina* and juvenile *Anapella* appear to segregate at lag zero in the autumn. The lack of directional bias in the associations indicate that the zonation of *Wallucina* and *Soletellina* are independent of the distribution of *Anapella*.

In contrast, *Wallucina* exhibits strong negative correlations with small or large *Katelysia* in all seasons. No directional bias is evident, however. *Katelysia* also interacts more strongly with *Soletellina*. Generally small *Katelysia* are involved and the correlations are positive. In the spring, however, *Soletellina* and large *Katelysia* appear to segregate. The relationships show no directional bias, indicating that the zonations of the two species are independent.

Anapella and *Hydrococcus* frequently show negative associations at zero lag, supporting the trophic group amensalism hypothesis. In spring, which is the season of strongest negative relationships, these correlations involve small *Anapella* and medium or large *Hydrococcus*. In the seasons of strongest interaction between *Anapella* and *Hydrococcus* - winter and spring - the two species show unidirectional relationships, with *Hydrococcus* being dependent on the the abundance of *Anapella* up the beach and *vice versa*. In other seasons, the associations are more bidirectional. Thus, in the seasons of major recruitment of *Anapella*, interactions with *Hydrococcus* appear to be at least partly responsible for the segregation of the two species along the transect. The other deposit feeding gastropod, *Salinator*, exhibits negative associations with small *Anapella* in all seasons. Those correlations have little directional bias.

The other major bivalve, *Katelysia*, shows particularly strong associations with *Hydrococcus*. Like *Anapella*, *Katelysia* has both positive and negative relationships with that gastropod and the strongest negative associations occur in spring. In that season, the abundance of *Hydrococcus* is dependent on the number of medium sized *Katelysia* further up the beach. Summer and autumn have similar directional bias at non-zero lags but the negative relationships are not as strong. There are no negative correlations in winter and the directional bias no longer occurs, suggesting that winter is the season of least segregation between the two species while the spring is the strongest.

Correlations between *Katelysia* and *Salinator* are not consistently negative like those involving *Anapella*. Negative correlations occur only in winter and spring and are strongest in the latter season. The negative associations involve large *Katelysia*, in contrast to the case with *Anapella*. Little directional bias is evident, suggesting that the zonation patterns are largely independent.

The associations between the suspension feeding bivalves and the deposit feeding gastropods can be considered in the light of the working hypothesis proposed for the maintainance of community structure in the lagoon. The segregation between the suspension feeding bivalves and the deposit feeding gastropods appears to be mutual. While the deposit feeding gastropods may exclude juvenile bivalves locally, the segregations between larger bivalves and the deposit feeders act in both directions. The segregations are strongest in the respective seasons of major recruitment of *Anapella* and *Katelysia*.

Anapella and *Zeacumantus* exhibit strong positive relationships at most lags. No serial correlations between *Katelysia* and *Zeacumantus* are significant. In winter and summer, however, large animals of *Anapella* and *Zeacumantus* are negatively

correlated. There is little directional bias in the associations, suggesting that the zonation patterns of the two species are independent. The strength of the correlations between *Anapella* and *Zeacumantus* are unexpected, given the apparent lack of dependence evident from the visual inspection of the distribution transect population structures.

Rissopsis appears to be positively correlated with medium and large *Anapella* in autumn and winter but the associations are negative in spring and summer. Only in the 200381 autumn does the zonation of *Rissopsis* appear to be affected by the distribution of *Anapella*. In that season the relationships are clearly defined and the distribution of *Rissopsis* is dependent on the abundance of *Anapella* further up the beach. The range of influence of *Anapella* increases with increasing body size. Negative associations between *Rissopsis* and small *Katelysia* occur in winter and spring while correlations are weak in the other seasons; no directional bias occurs.

Most associations between a number of *Anapella* groups and *Austrocochlea* are negative at zero lag, indicating a spatial separation between the two species. The relationships are strongest in autumn and winter. In those seasons the correlations are unidirectional, with *Anapella* being dependent on the abundance of *Austrocochlea* further down the beach or *vice versa*. Negative associations also occur between *Austrocochlea* and small *Katelysia*. These are strongest in spring and summer but there is little directional bias.

In all seasons, then, both *Rissopsis* and *Austrocochlea* show segregation with one or other of the major bivalves.

Microdiscula and medium or large *Anapella* are positively associated at zero lags in all seasons but summer. There is no evidence of bidirectionality in the relationships. In contrast, there are negligible relationships between *Katelysia* and *Microdiscula*.

Bembicium is negatively correlated with *Anapella* in autumn but in other seasons the is little relationship between the two species (correlations between *Bembicium* and *Katelysia* are never significant). There is no evidence of directional bias in the associations. This may be a reflection of the very restricted zone of *Bembicium* which only covers two or three sample intervals - there could be an insufficient number of non-zero data points to detect bias.

There is little directional bias in the relationships between *Anapella* and *Notoacmea*. Zero lag correlations are positive and this may be partly due to an occasional tendency of *Notoacmea* to use large *Anapella* as a substrate. Similar factors would account for the strong positive correlations between *Anthopleura* and large *Anapella*.

Anthopleura and *Notoacmea* do not use *Katelysia* as a substrate as frequently as

they use *Anapella*. In fact, *Notoacmea* was never observed to be epizoic on *Katelysia*, although the animals may have been separated during sampling. *Anthopleura* was often found on large *Katelysia* but during sampling it was noted that the anemone was easily disloged from *Katelysia*. This is probably due to the shell striations of those bivalves which would prevent the anemones (and limpets) from gaining a firm attachment.

The differences in the use of *Katelysia* as a substrate are evident in the serial correlations between *Notoacmea* and *Katelysia*. In summer and spring the two species are negatively correlated, indicating a spatial segregation. In the other seasons, however, *Notoacmea* tends to be positively associated with large *Katelysia*. Similarly, *Anthopleura* and *Katelysia* are negatively correlated in winter, although the relationships are positive in the other seasons.

In the previous chapter it was suggested that the distribution of *Agatha* could be related to that of *Anapella*, possibly as a parasite-host association. However, the two species show positive correlations (involving large *Anapella*) at zero lags only in autumn. In the other seasons the relationships are weak. Similarly, *Agatha* and *Katelysia* are only weakly correlated. It is not possible from these observations to suggest any host-parasite relationship between *Agatha* and the major bivalves.

Cylichnina shows positive correlations with juvenile *Anapella* or *Katelysia* in most seasons. Juvenile bivalves are known to be a food source for a number of Retusidae (see Chapter 2) and these correlations may indicate a trophic relationship between the species. The strength of the association with *Anapella* appears to be sufficient to influence the winter and spring distributions of *Cylichnina*. These seasons have an abundance of juvenile *Anapella* and the abundance of *Cylichnina* is influenced by the numbers of adult *Anapella* up the beach as is the abundance of *Anapella* juveniles. In summer *Cylichnina* and large *Katelysia* appear to segregate along the transect, with negative correlations occurring at zero lags. In autumn there is a similar association involving small *Katelysia*. This indicates that *Anapella* is a more likely food source for *Cylichnina*.

As mentioned in Chapter 2, *Nassarius* was frequently seen preying on medium and large *Anapella* and this is evident in the series analysis. *Nassarius* shows a general positive relationship with those animals but this is not sufficient to affect the zonation of either species. The relationship between *Nassarius* and *Katelysia* is less defined, again suggesting that *Anapella* is a more important food source.

The deposit feeding bivalve, *Soletellina*, shows comparatively strong relationships with the deposit feeding gastropods, *Hydrococcus* and *Salinator*. In most seasons

Soletellina and *Hydrococcus* are positively associated and often the abundance of the gastropod is dependent on the numbers of *Soletellina* further up the beach. The correlations between *Soletellina* and *Salinator* are less defined, but tend to be negative. Although *Soletellina* occasionally exhibits significant associations with other species, the relationships are generally weak and inconsistent.

The two most abundant deposit feeding gastropods, *Hydrococcus* and *Salinator*, show positive relationships. Only in winter does there appear to be spatial segregation. In all seasons the zonations of the two species exhibit interdependence, with the abundance of *Salinator* being related to the numbers of *Hydrococcus* further up the beach and *vice versa*. The non-zero lag associations are comparatively weak in autumn and winter, however.

In summer and autumn, *Salinator* and *Zeacumantus* appear to segregate on the tidal flat but their relationship does not extend to influence the zonation patterns of either species. *Salinator* does not exhibit strong relationships with any of the remaining species.

There is evidence of spatial separation between *Hydrococcus* and *Zeacumantus*. In most seasons there are correlations betwen the abundance of *Zeacumantus* and the numbers of *Hydrococcus* further up the beach. Except in the 200381 autumn and in winter, the two species have negative associations at zero lags and these occur between a range of size groups from each species.

The serial relationships between *Hydrococcus* and the remaining species are relatively weak. Given the working hypothesis, *Hydrococcus* might be expected to show strong relationships with *Cylichnina* and *Anthopleura* (likely predators). This does not occur, however. As noted in the previous chapter, *Hydrococcus* and *Cylichnina* have similar zonation patterns; the series analysis indicates that this is not necessarily due to a functional relationship.

Similarly, although *Anthopleura* was observed to feed on *Hydrococcus*, that predation does not influence the distribution of either species along the transect. It is important, however, to recognise the dependence of *Anthopleura* on *Anapella*, which provides the anemone with a substrate. Because of that relationship, it is unlikely that *Anthopleura* could be involved in any dynamic zonation associations. The range of influence of *Anthopleura* would be greatly restricted by its sessile habits. If functional relationships between those species do exist, they are too weak to be detected at the scale of the analysis.

Zeacumantus does not show consistent associations with the other algivores. In

summer and in the 310382 autumn, however, *Zeacumantus* and *Rissopsis* tend to be found together. In those seasons the distributions of *Zeacumantus* and *Bembicium* are also related, with the sign of the correlations being negative. There is some suggestion that the distribution of *Microdiscula* is affected by the abundance of *Zeacumantus* further up the beach; in the 310381 autumn ,the two species appear to segregation along the transect.

The series analysis indicates a somewhat surprising association between *Zeacumantus* and *Agatha*. Those species show significant correlations at lag zero in all seasons, although the sign of the correlations varies from season to season. The relationships are negative in the 200381 autumn, the winter and the summer and are positive in the other seasons. It was previously suggested that *Anapella* was the most likely host for *Agatha*. However, those two species show little serial correlation and it now appears that *Zeacumantus* is a more probable host. As was shown in the previous chapter, *Zeacumantus* and *Agatha* have similar zonations but the lack of directional bias in the serial correlations at non-zero lags indicates that those zonations are not actively maintained.

The weak relationships among the remaining species indicate that their distributions along the transect are independent of each other.

The following chapter examines the intra- and interspecific associations over much shorter distances (measured in centimetres, rather than metres) and represents the next step in the hierarchical testing of the relationships.